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DESERT LOCUST MIGRATIONS AND SYNOPTIC METEOROLOGY IN THE GULF OF ADEN AREA

BY R. C. RAINEY AND Z. WALOFF, *Anti-Locust Research Centre, London*

(With 6 Figures in the Text)

1. INTRODUCTION

Swarms of the desert locust, *Schistocerca gregaria* (Forskål), have been recorded arriving on the coasts of the Somalilands and southern Arabia on a number of occasions, and particularly comprehensive records of such movements have been secured by the locust control organizations in the course of the recent outbreak (1941–7). The origin of these swarms is a matter of substantial practical importance, while such movements are also of considerable interest in relation to the fundamental problem of locust migration.

From the nature of the problem it is clear that a detailed study of the meteorological factors likely to affect a flying swarm requires much more than observations at a single point on the ground. Data on wind, temperature, etc. are in fact required for the whole area traversed by the swarm, and up to altitudes at times of the order of 10,000 ft. Very fortunately, these are also the basic data of synoptic meteorology, which are required for the preparation of weather forecasts; and, through the courtesy of the Senior Meteorological Officer, Aden, it has been possible to examine the synoptic charts recording current meteorological conditions over the whole area around the Gulf of Aden for a number of occasions on which interesting swarm movements were recorded. The present investigation has incidentally been largely made possible by the substantially augmented surface and upper-air observations which were needed to meet the wartime requirements of aircraft and shipping in this area.

In considering the various possible areas of origin of a particular swarm in relation to the current weather conditions, one may obviously exclude those areas migration from which would encounter head winds exceeding the flying speed of the locusts. Recent determinations (not yet published) of the flying-speed of *Schistocerca* in the field in Somalia, made by the present authors, gave a frequency distribution of normal type centred at about 11 m.p.h., in close agreement with an estimate of 9 knots obtained by J. F. Graham in Kenya by a different method (quoted by Gunn, Perry, Seymour, Telford, Wright & Yeo, 1948). These values provide a useful indication of the strongest wind against which swarm movements are possible, though temperatures were in the region of 85° F. in both cases, and similar observations over a wider range of conditions are clearly required.

Furthermore, the route of one particularly well-documented long-distance flight by a swarm of this species (from southern Morocco to Portugal) was recently shown to correspond closely with the trajectory of the air-mass in which the flight began (Waloff, 1946*a*), indicating the great importance of the air movement compared with the locusts' own movement relative to the air. It was therefore hoped that the construction of similar trajectories for the Gulf of Aden records might throw further light on the origin of these swarms.

Variations of wind with height tend largely to disappear under the influence of active convection, though surface friction still causes some reduction of speed (and deviation down the barometric pressure gradient) in the lowest few hundred feet. In view also of the part probably played by convection currents in swarm movements (see p. 111, etc.), there is added reason for regarding the wind at 1000–2000 ft. as a reasonable estimate of the wind normally concerned in long-distance swarm movements, even though such movements may sometimes take place at considerably greater heights. Flight at much lower levels has been observed, for example, in the Kenya Highlands, but was associated with relatively low temperatures and with displacements of a few miles a day (Gunn *et al.* 1948), and appears unlikely to play much part at any rate in rapid long-distance swarm movements.

The possibilities of constructing trajectories in the Gulf of Aden area are limited by the proximity to both coasts of mountains over 6000 ft. high, and, in the absence of the very full upper air data necessary to estimate the ascent or descent of the air masses involved, attention has been confined to constant-level trajectories over the sea and the coastal plains.

The interpretation of observations on both weather and locusts in this area has been facilitated by the fact that, while diurnal variations of wind, temperature, etc. are large and striking, day-to-day variations in weather are usually relatively insignificant, since the

Gulf is well clear of the normal tracks both of temperate depressions and of tropical cyclones. This high degree of regularity of the weather, and in particular of the winds, encouraged the hope that swarm movements might show a similar regularity, and that it might be possible to fit together the inevitably fragmentary observations on individual swarm movements into a satisfactory composite picture.

A general scheme of seasonal migrations of desert locust swarms in this area will be found in a recent publication by Waloff (1946*b*).

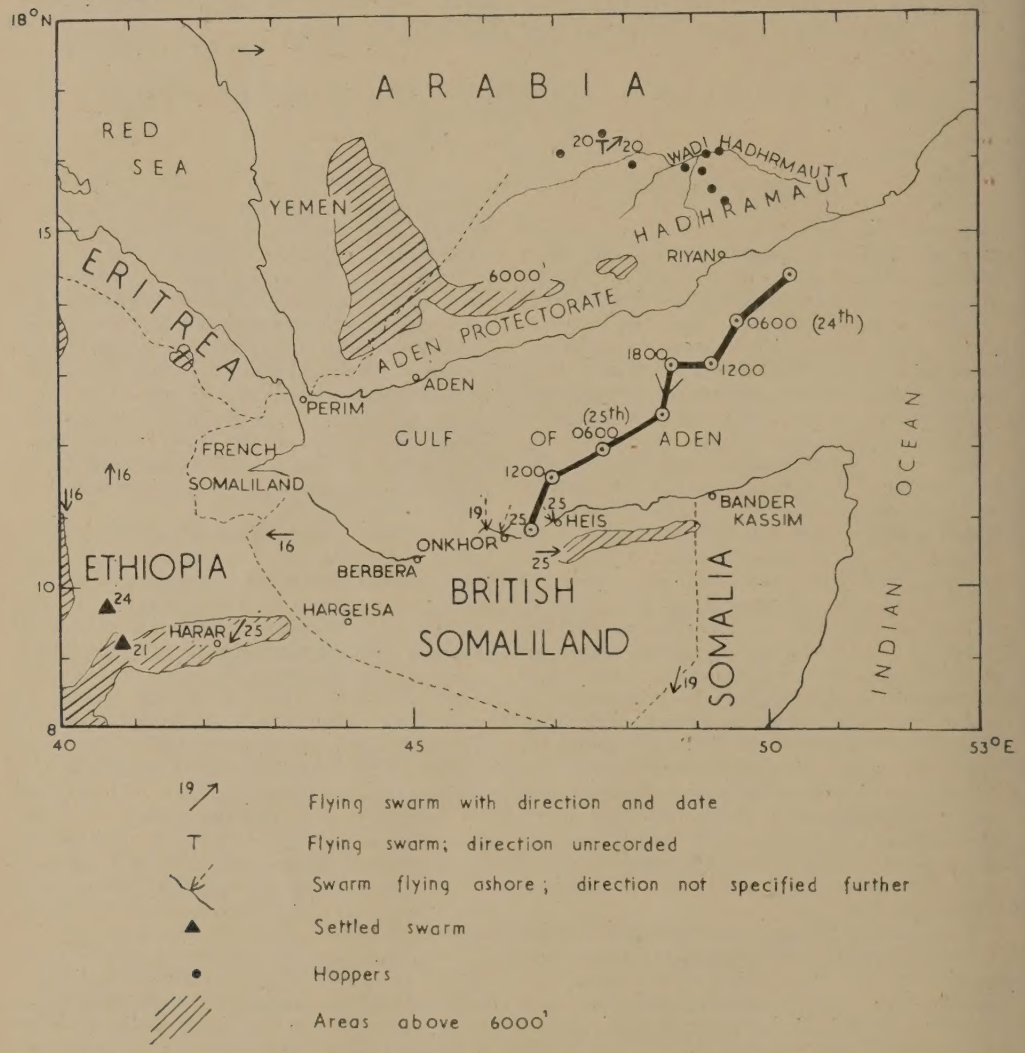

Fig. 1. Distribution of swarms, red and of unrecorded colour, for 15–25 October and of hoppers for 1–15 October with 2000 ft. trajectory of air reaching Heis-Onkhor area at 15.00 hr. on 25 October 1945.

2. SWARM MOVEMENTS DURING THE NORTH-EAST MONSOON

On 19, 25 and 27 October 1945, swarms were reported arriving from the north on the British

Somaliland coast between 46° and 47° E.; there were many dead on the foreshore and 3–4 miles inland. On 25 October, which may be taken as representative of this period, immature (red) swarms were reported flying ashore near Heis and Onkhor (Fig. 1). At this period British Somaliland was otherwise practically clear of red swarms, which were, however, present in Somalia (El Bur area), Ethiopia (Harar plateau and Danakil), Eritrea (plateau and coast), and Arabia (just north of Wadi Hadhramaut). North-easterly winds of substantial depth approaching 20 m.p.h. at Hargeisa and Berbera on the afternoons of the 24th and 25th ruled out migration from Somalia or Ethiopia, while southerlies of similar strength at Perim eliminated Eritrea. A 2000 ft. trajectory, based on upper wind observations at Aden, Riyan, Berbera and Bander Kassim, indicates that the air which reached the Onkhor-Heis area at this level at 15.00 hr. (local time used throughout) on the date of arrival of the swarms had been about 50 miles off the mouth of Wadi Hadhramaut some 40 hr. previously; and the dew-point of 56° F. recorded at Riyan at 15.00 hr. on the 23rd (normal 15.00 hr. value for October 74°) strongly suggests air from the interior of Arabia. It would thus appear almost certain that these swarms were Arabian late Monsoon generation, derived from the widespread hopper infestation reported in Wadi Hadhramaut and its tributaries in September and early October 1945. Upper wind studies, such as those of Ramanathan and Ramakrishnan (1939), and synoptic experience suggest that the air over the Gulf of Aden during the North-East monsoon originates usually from north-west India or the Gulf of Oman, and only relatively rarely from the interior of Arabia as in this instance. This may perhaps explain why such swarm movements have not been recorded more frequently.

A similar case was recorded on 14 December 1945, when a high-flying swarm was observed over the sea off Berbera at dusk, apparently circling (Fig. 2). Swarms were present in southern Somalia, Ethiopia, Eritrea, Yemen, Aden Protectorate, Hadhramaut and southern Persia, as well as in British Somaliland. The monsoon was more strongly established than in the October case, and air reaching Berbera at 2000 ft. at dusk on 14 December had been within 30 miles of the Hadhramaut coast only 18 hr. previously.

The record of the time of arrival of this swarm makes possible a more rigorous investigation of its origin, as follows. Assuming that the trajectory adequately represents the winds experienced by the swarm, then, for as long as the locusts had remained airborne, and whatever their 'course' or orientation, their position at any time previous to their arrival at Berbera must have been within a circle centred at the point on the trajectory corresponding to this particular time, of radius equal to the distance which the swarm could have flown in still air over the intervening period. Fig. 2 shows such a circle for a time 18 hr. before the swarm was reported off Berbera and based on an air-speed of 11 m.p.h.; this circle includes an area of the Hadhramaut (cross-shaded in Fig. 2) within which swarms had recently been reported. Subject to the foregoing assumptions, a flying swarm which had been at any point on the circumference of the circle at 24.00 hr. on the 13th, and had maintained the course given by the corresponding radius (as indicated by the tailed broken arrows), would have reached Berbera at 18.00 hr. on the 14th, as would also a swarm starting at the same time at the centre of the circle and either making frequent random changes of course or circling continuously; the track of such a swarm would, in fact, correspond with the trajectory itself. Furthermore, when visual perception of features of the substratum is possible, for example, up to probably relatively moderate heights over land by day, negative components of ground-speed are unlikely to be tolerated (Gunn *et al.* 1948), and in such circumstances this circle could be reduced to a semi-circle as indicated.

The positions farthest from the trajectory correspond to the maintenance of courses 90° on either side of the mean wind direction. The broken lines connect a series of such points for successive times, and thus enclose all possible positions of the swarm over the period indicated (these areas are shown in Fig. 2 by vertical shading), thereby excluding the possibilities of migration from southern Somalia, Ethiopia, Eritrea, the Yemen or the western Aden Protectorate. It will be noted, however, that the swarm could have come from the Erigavo area, where swarms were present at this period, by maintaining a north-north-westerly course. However, in the case of another long-distance swarm movement (p. 111), sufficient information is available to demonstrate that a similar cross-wind course was not in fact maintained, and on balance it is therefore perhaps most likely that the Berbera swarm in question had come from the Hadhramaut. It could in this case have been either late Monsoon generation produced in south-west Arabia, or Monsoon generation which had been produced in Eritrea or north-east Ethiopia and had migrated to Arabia between October and December.

3. SWARM MOVEMENTS DURING THE SOUTH-WEST MONSOON

(*a*) *Movements concerning the north coast of the Somali peninsula*

Swarm movements around the Gulf of Aden during the South-West monsoon of the summer months are well exemplified by the period 20–30 June 1946 (Fig. 3). A red swarm was reported coming on shore

at Aden sometime between the 25th and 27th. The 26th was characterized by fresh south to south-westerly winds, and air reaching Aden at 1500 ft. that afternoon had travelled at 20 m.p.h. from a position over the western Guban (coastal plain of British

noon with a west-south-westerly wind may be attributed to dust carried up by vigorous convection inland, which is likely to have facilitated the flight of these swarms. It is therefore highly probable that locusts reaching Aden during the afternoon of the

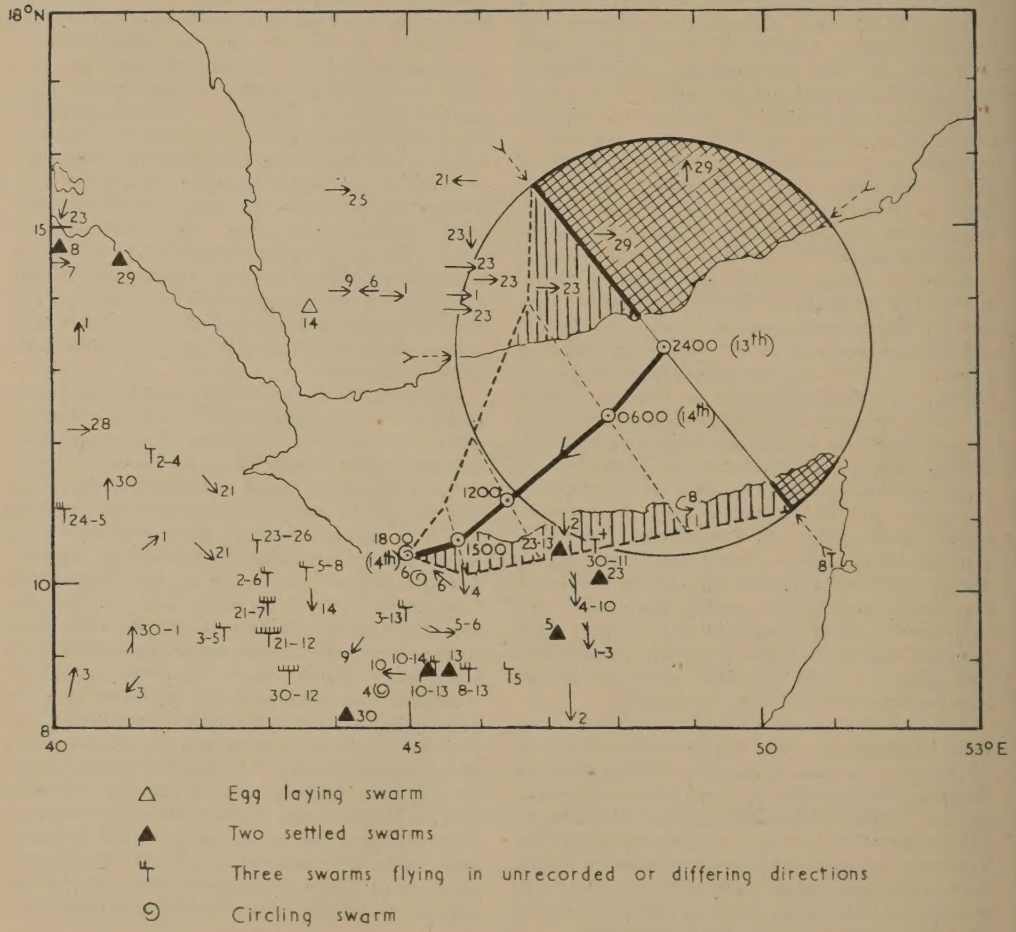

Fig. 2. Distribution of all swarms for 21 November–14 December with areas of probable origin of swarms seen off Berbera at dusk on 14 December 1945 (for full explanation see text).

Somaliland) some 10 hr. previously. A considerable number of red swarms were recorded in this area in the course of the previous week, and five were reported flying in a north-easterly direction on the 26th itself in western British Somaliland and the adjacent parts of Ethiopia. The haze reported at Berbera at

26th had left western British Somaliland the same morning, and were Long Rains generation produced in eastern Ethiopia or the northern Somali peninsula. Other swarms were reported on the Arabian coast east of Aden on the same day, and may well have been transported similarly. It may be mentioned that at

this season Aden often experiences a dust haze which is similarly of African origin, brought in by freshening south-westerlies at about 03–04.00 hr. It is, however, unlikely that all the swarms reported as moving north-eastward on the 26th in western British Somaliland subsequently reached Arabia, owing to the characteristic diurnal variation of the wind at this season, which 'is not merely a local phenomenon confined to the coasts but extends also over the sea and is felt up to a height of some 3000–4000 ft.' (Meteorological Office, 1944). This sea-breeze effect developed later than usual on the 26th, afternoon. Swarms moving in a north-easterly direction were reported from four localities between Borama and Sheikh on the 20th, and some of these too may have followed courses similar to that indicated by the trajectory for this date. Small yellow (mature) swarms were also reported as 'blown out to sea' at Bulhar and Berbera on the 17th and 19th respectively.

A red swarm was reported coming ashore at Karin on about the 25th, and another was seen offshore between Heis and Mait on the 30th. The Berbera upper-wind observations were incomplete on these

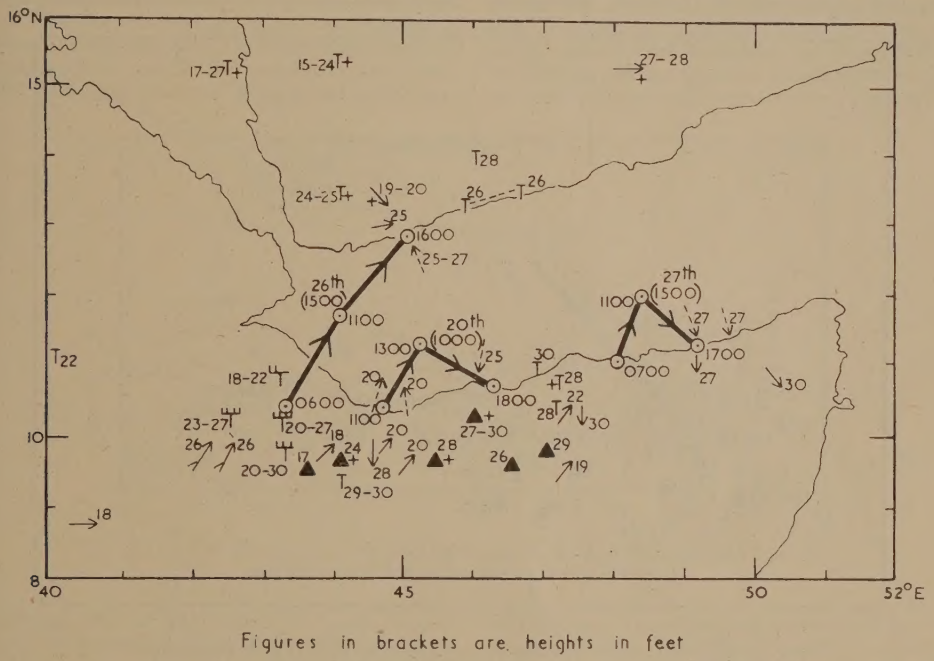

Fig. 3. Distribution of all swarms for 15–30 June 1946, with some representative air trajectories.

but a light north-westerly breeze was established at Berbera by 18.00 hr., and may have been sufficient to bring back swarms swept seawards in the late afternoon.

This latter effect is illustrated in a more marked manner by the data of the 20th, when swarms were observed flying out to sea between Berbera and Bulhar. With a south-south-westerly wind just short of gale force at 1000 ft., swarms crossing the coast in the early morning may well have reached Arabia, but the sea breeze came in earlier than on the 26th, and air crossing the coast in this area at 11.00 hr. would have come in again in the vicinity of Karin in the late dates, but the surface wind data suggest that these swarms may also have come in with the sea-breeze after having been carried out by the south-wester, which is known locally as the Kharif. The swarm recorded on the 30th was in fact reported as 'probably blown out (to sea) and returning.' 24 and 29 June, the days preceding these swarm records, were the only dates on which rising sand was recorded at Bandar Kassim during the month, and, if the associated strong offshore winds (south, 30–36 m.p.h.) and intense convective activity were also experienced farther west, both these factors may have been involved in initially carrying the swarms seawards. An

association between locust movements and dust-storms has already been recorded in north-west India (Bhatia, 1939).

On the 27th red swarms came ashore at Bander Kassim and Kandala. Upper-wind observations indicate that air reaching Bander Kassim at 1500 ft. in the late afternoon was over the British Somaliland coast to the west that morning. A swarm was in fact reported a few days previously in the vicinity of Erigavo, moving north-eastwards, and it is probable that at this period not only Arabia but also the Mijertein province of Somalia were receiving swarms from British Somaliland via the Gulf of Aden. Dhow crews

40 m.p.h. at 1500 ft., and air arriving at Aden at this level during the afternoon had been over the western Guban some 5 hr. previously (Fig. 4). At this period there were numerous swarms of the Long Rains generation in British Somaliland and the adjacent parts of Ethiopia, and the Aden swarm therefore may well have come from this area. The same swarm was later reported flying out to sea on the 18th, when winds were again southerly at the surface and south-westerly above, becoming 210°, 30 m.p.h., at 1500 ft. in the afternoon. The Aden peninsula has the sea on all sides except north and north-north-west, and it is highly probable that this swarm subsequently came

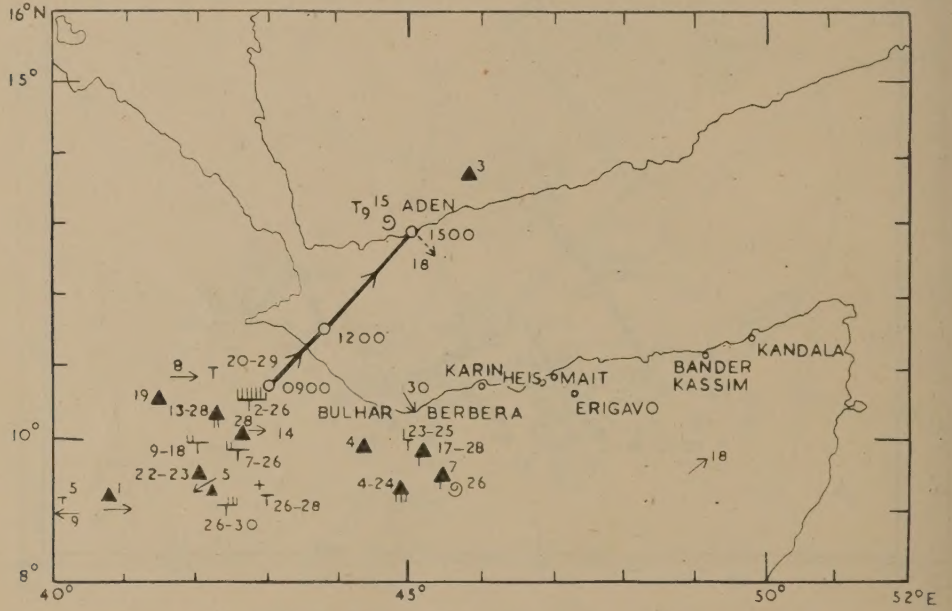

Fig. 4. Distribution of all swarms for 1–30 August, with 1500 ft. trajectory of air reaching Aden on 15 August 1943.

reported sighting many swarms at sea in the Gulf of Aden in late June and early July; and, when allowance is made for the necessarily attenuated locust reporting service resulting from the customary seasonal emigration of the native population out of the coastal areas, the extensive scale of these swarm movements becomes apparent.

A number of other swarm records relating to the north coast of the Somali peninsula for the period of the south-west monsoon have been investigated, and each appears to correspond to one or other of the foregoing examples. Thus on 15 August 1943 a swarm was reported circling at Aden; surface winds were southerly, with fresh south-westerlies above, reaching

ashore again on the Arabian coast somewhere east of Aden. The only noticeable weather change recorded at Aden between the 15th and 18th was a gradual increase in convective activity, which may have played some part in the final departure of the swarm. Thus, while the afternoons of the 15th and 16th were cloudless, small amounts of cumulus congestus cloud were present on the 17th, and of cumulo-nimbus on the 18th. Upper-air temperatures similarly showed conditions to be least stable on the 18th, with no lapse-rate less than the saturated adiabatic anywhere between 970 and 500 mb. as there had been on each of the preceding 3 days, and a surface maximum of 93° F., 1–2° higher than on the preceding days—which

may also of course have affected the activity of the swarm directly.

On 30 August a medium swarm, flying high, was reported coming in from the sea at Berbera. A south-west wind of 26 m.p.h. was recorded at 05.00 hr., decreasing to south-west 10 m.p.h., by 15.00 hr., when visibility was reduced by haze to 1 mile (the lowest figure recorded for the month), indicating marked turbulence inland. There were no later observations to record the development of the sea-breeze, but in the circumstances it appears most likely that the swarm reported coming in from the sea had been blown offshore by the strong and turbulent wind the same morning. Numerous swarms were reported in western British Somaliland and the adjacent parts of Ethiopia at this period. The recorded surface winds make it unlikely that the Berbera swarm had any connexion with the Aden report of 12 days earlier, though the possibility of high-level migration across the Gulf (see p. 109) cannot be entirely excluded, and does in fact receive some support from the fact that the inter-tropical front was just south of Aden on the morning of the 30th, indicating some advance of the upper north-easterlies at the expense of the lower south-westerlies.

On 25 June 1944 a mature swarm was reported flying northwards and settling just inland from Ras al Hadd, easternmost point of Arabia, where winds were strong south-south-westerlies at first, with a moderate east to south-east sea-breeze later in the day. There had been a south to south-west wind of 25–30 m.p.h. all the previous day, with a sand-storm at midday reducing visibility to 200 yd. at times; sandstorms were recorded at Ras al Hadd on five other days during the month, but only once of similar intensity. It appears likely that this swarm, like the African ones already discussed, was carried seawards by the combination of a strong offshore wind with vigorous convective activity inland, and subsequently brought in again by the sea-breeze.

On 7 June 1945 a mature swarm was reported coming in from the sea at Bander Kassim. There were no reports of mature swarms in Arabia south of 20° N. at this period, but mature swarms of the Short Rains generation were widely distributed over Somalia. The southerly monsoon at Bander Kassim on the 7th was as usual replaced by a north-westerly sea-breeze during the afternoon; an approximate trajectory (Fig. 5) constructed from the available surface, and upper-wind observations again demonstrates that the air reaching Bander Kassim in the late afternoon had been over the coastal plain not far away to the west the same morning. The surface temperature at 09.00 hr. was already 97° F., well above the value needed for the locusts to become airborne. It may therefore be suggested that this particular swarm was also swept out to sea by the monsoon in the morning and brought back by the sea-breeze in the afternoon. In view of the active convection over the land under these conditions, and its absence over the sea, locusts returning with the sea-breeze might be expected to cross the coast at a lower altitude than when outward bound, and might hence be more readily observed, though on the 11th another mature swarm was in fact reported flying out to sea some 20 miles west of Bander Kassim.

On 3 July 1946 a mixed swarm was seen flying south-eastwards over the sea between Onkhor and Heis. A 1500 ft. trajectory (Fig. 5) indicates that air at this level in this area at 16.00 hr. on this date would have left the coast in the vicinity of Bulhar some 8 hr.

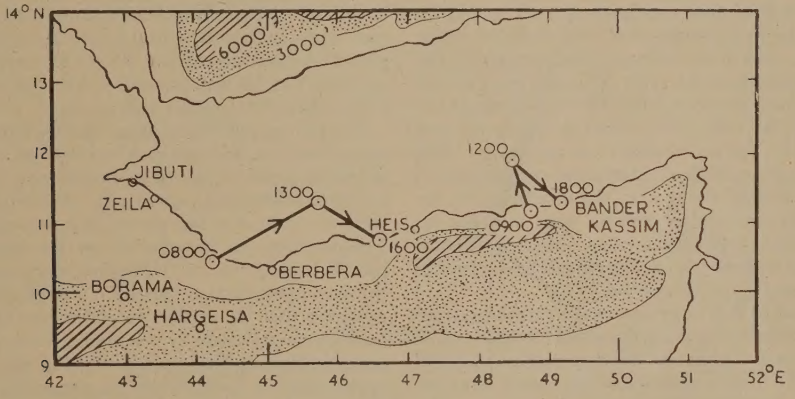

Fig. 5. 1500 ft. trajectories of air reaching Bander Kassim at 18.00 hr. on 7 June 1945, and Heis-Onkhor area at 16.00 hr. on 3 July 1946.

previously, travelling at 20–25 m.p.h. The north-westerly sea-breeze was established at Bander Kassim before midday, but did not set in at Berbera until several hours later, indicating that a similar trajectory would have been followed for a considerable part of the day. It may incidentally be noted that the recorded direction of flight of the swarm was also the direction of the sea-breeze. The haze reported at Berbera at midday, while the south-wester was still blowing, suggests vigorous convection inland, and the similar haze recorded at the same time at Bander Kassim coming in with the sea-breeze provides further evidence of the origin of the latter. Mixed swarms were reported in the course of the preceding week in the mountains south of Bulhar, and this area may well have provided the swarm under discussion.

On 21 July 1946 mixed swarms were reported coming ashore at Mait and farther east; the same morning Berbera had experienced a 40–45 m.p.h. gale from the south-south-west, with visibility down to 1000 yd.; and mixed swarms were reported in the Zeila-Borama area in mid-July. The only other record of rising sand at Berbera during the month was on the morning of the 11th, with a south-westerly wind of 25–30 m.p.h., and a red swarm was reported coming inland at Karin next day; red swarms were present in the Borama-Hargeisa area at the beginning of the month. Well-marked sea-breezes were recorded on the afternoons of the 12th and 21st at Bander Kassim (though not at Berbera), and may well have brought in the swarms under discussion.

On 18 and 19 July 1947, red swarms were reported coming in from the sea along the whole British Somaliland coast east of Heis; on the mornings of the 17th and 18th the first sandstorms of the month were recorded at Berbera, with winds of 20–30 m.p.h., followed by west-north-westerly to north-westerly sea-breezes of 5–10 m.p.h. in the afternoons. At this period red swarms of the Long Rains generation were widely distributed in British Somaliland, and these records also may be attributed to such swarms of local origin.

The fact that no swarms have been recorded coming ashore west of Berbera may perhaps be associated with the apparent absence of a sea-breeze at Jibuti during the south-west monsoon (Meteorological Office, 1944).

(b) Movements on the east coast of the Somali peninsula

There are a number of records of swarms coming ashore on the coast south of Cape Guardafui during the south-west monsoon, but unfortunately corresponding meteorological records for this area are available only for 1 month (June 1944).

A mature swarm was reported flying inland from the coast near Ghirbirli, between Bargal and Ras Hafun, on 5 June 1944. At Iskushuban, the nearest meteorological station, winds were south-westerly, 5–15 m.p.h., all day on the 5th. The previous day rising sand was reported from 08.30 to 11.00, with winds of 260–270°, 20–32 m.p.h., from surface to 4000 ft. at 09.15. By 15.30 the wind had dropped to 250–290°, 7–15 m.p.h., up to 8000 ft. and became north-north-east, 2 m.p.h., at the surface at 21.00. Winds between north-north-east and south-east at 21.00 were similarly recorded during this month on six other days, which probably represent occasions when the sea-breeze was strong enough to reach Iskushuban, 40 miles inland, against the monsoon. Thus no easterly wind was recorded at any other time of day during the month; and the absence of any break in the monsoon was shown by the surface winds at Socotra, which were continuously south to south-south-west, 10–30 m.p.h., from the 1st until the 5th. Furthermore, ship reports in long. 53° E. on the 4th gave west-south-west, 10 m.p.h., in lat. 10° N. and west-south-west, 5 m.p.h., in lat. 11½° N., and aircraft at 1800–5000 ft. on the 5th reported winds of 240–300°, 17–28 m.p.h., at a series of points 30–90 miles offshore between 7 and 12° N.

Thus the possibility of long-distance low-level immigration from overseas may be ruled out, and, while at higher levels (8–10,000 ft.) winds were north-east to east-north-east, 15–30 m.p.h., no mature swarms were reported over this period in south-east Arabia. Temperatures at Iskushuban on the 4th and 5th ranged from 77 to 104° F., sufficiently high for continuous flight, and on balance it would appear most probable that the swarm recorded on the 5th had been swept seawards by the strong westerlies of the previous day, in conjunction with the vigorous convective activity indicated by the rising sand, and was then carried ashore again by the particularly well-marked sea-breeze that evening. Mature swarms of the Short Rains generation had been reported from eastern British Somaliland and the central Mijertein a few days previously.

On 24 June 1944 mature swarms were reported flying southwards on the coast near Ras Hafun, and flying south and west at and near Bargal. At Iskushuban on the 23rd a gusty south-south-westerly wind of 25–30 m.p.h. (the highest wind recorded during the month) raised sand and dust locally between 09.00 and 11.00 hr., reducing the visibility to 2½ miles; rising sand with a similar or worse visibility was only recorded at Iskushuban on two other days during the month besides the 4th and 23rd. The wind dropped to south-west 10 m.p.h. by 15.00 hr., and the development of the sea-breeze is suggested by a northerly wind of 15 m.p.h. at Bander Alula at the same time. The Socotra upper winds give no indication of any break in the monsoon, being 190–250°, 20–50 m.p.h. up to 3000 ft. over the whole period 20–24 June. It is therefore suggested that these swarms also were

probably carried seawards by the strong and turbulent monsoon of the 23rd and brought back and down the coast by the subsequent sea-breeze.

Other landings on the Somalia coast between Cape Guardafui and Bander Beila during the South-West monsoon were recorded on twelve occasions during 1945, 1946 and 1947, and while no local meteorological data are available, the fact that similar swarms were known to be already present in Somalia on all save two of these occasions (in July 1945) suggests that such coastal swarms may frequently be of local origin.

ously south-west to south-south-east, 15–50 m.p.h., for the whole month, excluding any possibility of migration from the north or north-east at low levels. The upper winds, however, indicate that at least some of the air reaching the Mijertein at 10,000 ft. may have been of Arabian origin. Thus (Fig. 6) air reaching Bander Kassim (where upper wind observations were made) at this level on the evening of 15 July was probably in the vicinity of Mukalla that morning. Swarms of the Arabian Spring generation were in fact reported in this area a few days previously, and were the nearest recorded swarms to the Mijertein.

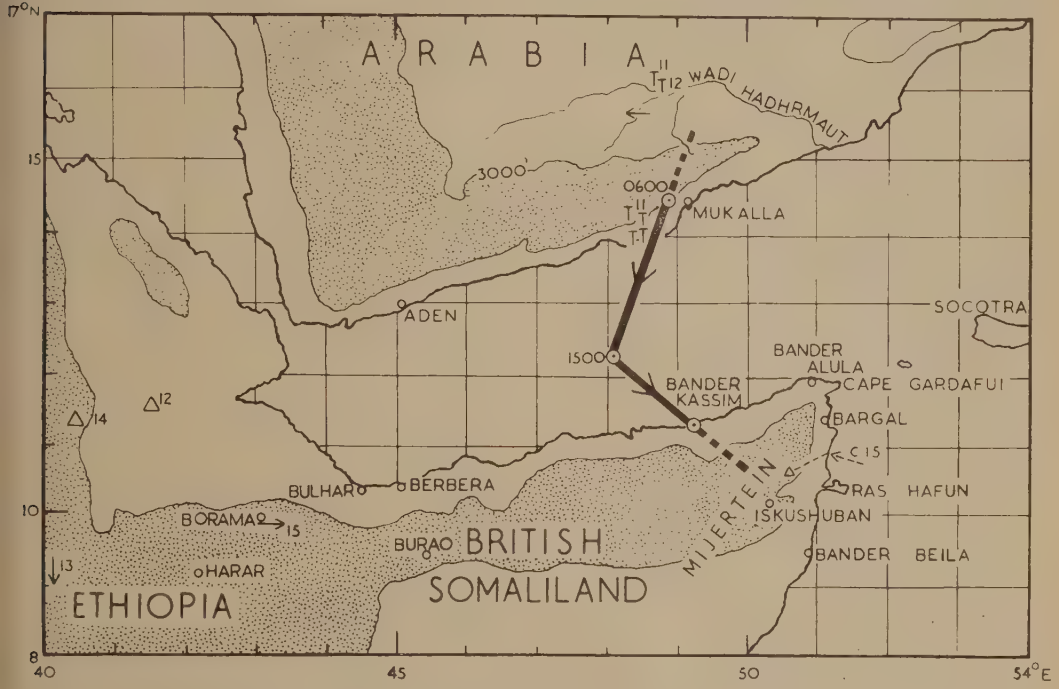

Fig. 6. Distribution of swarms, yellow and of unrecorded colour, 1–15 July 1945, with 10,000 ft. trajectory of air reaching Bander Kassim at 24.00 hr. on 15 July.

An alternative possibility in some of these cases is that of transportation by the north-easterlies which overlie the south-west monsoon and are probably continuous with the surface north-westerlies of Arabia at this season (Meteorological Office, 1944). Thus, for example, in mid-July 1945 a mature swarm flew in from the sea between Bargal and Ras Hafun, and numerous drowned locusts were recorded on the shore in the same area a few days later; Somalia and British Somaliland east of 44° E. were reported otherwise clear. Surface winds at Socotra were continu-

Locusts reported in large numbers at 7000 ft. by a B.O.A.C. aircraft near Bulhar on another occasion (10 August 1946) indicate the possibility of high-level migration. The air temperature recorded by the aircraft at the same time (72° F.) demonstrates a lapse-rate approaching the dry adiabatic from the corresponding surface reading at Berbera (104°), indicating unimpeded convection currents, extending from the coastal plain to at least the height of the locusts, which may well assist in initiating such flights. Direct determinations of the vertical extent of convection

currents in the Transvaal have been found to agree closely with the theoretical upper limits of such currents given by the corresponding upper-air temperatures (Rainey, 1947). The Aden upper-air temperatures on 15 July 1945 show a lapse-rate close to the dry adiabatic from 800 to 540 mb., suggesting free convection from plateau level over Arabia; the temperatures of 62–63° recorded at 10,000 ft. would also permit active flight (Gunn *et al.* 1948).

However, winds of 200–290°, 20–45 m.p.h. 2000 ft. above Hargeisa during 10–20 July, suggest the further possibility of migration from the Harar plateau, where mature swarms were also present; the absence of reports from intermediate points might be partly explained by speed of movement (Hargeisa–Ras Hafun at 35 m.p.h. would require some 20 hr. flying, which might easily take place in the course of 2 days).

The first swarm to be recorded on the Somali peninsula at the beginning of the 1941–7 swarming period was reported at Ras Hafun on 7 September 1941. Winds at Burao (the only point in the peninsula from which corresponding meteorological records are available) were south-west to west-south-west, 5–30 m.p.h., for the whole of September. On the 6th the monsoon was reported moderate to strong over East Africa, and at 09.00 hr. rising sand, following a sandstorm, was reported at Burao, with a south-west wind of 25–30 m.p.h. and visibility reduced to 2½ miles; sand-storms were only recorded on two other days during the month. A swarm was reported just west of Borama on the 6th and, while any conclusion from such scanty meteorological data must obviously be treated with reserve, it may be tentatively suggested, by analogy with later observations, that this Ras Hafun record may refer to a similar but hitherto unreported swarm of the monsoon generation from the interior, brought down to the coast by the Kharif, though it is not possible to exclude the alternative possibility of the high-level migration of an Arabian monsoon swarm derived from the hoppers which were reported in the upper Wadi Hadhramaut in August and September 1941.

4. DISCUSSION

A number of the records investigated provide evidence of the exchange of swarms between Arabia and Somali peninsula suggested by Waloff (1946*b*), though with considerable differences in detail. Thus the records of June 1946 and August 1943 indicate the immigration into the Aden Protectorate from western British Somaliland of swarms of the Long Rains generation produced in eastern Ethiopia or the northern Somali peninsula. Such arrivals would participate in the monsoon breeding which may take place in southern and south-western Arabia between July and October. The records of October and December 1945 provide evidence of the immigration into British Somaliland from the Hadhramaut of swarms of the monsoon generation, either produced in southern Arabia or derived from Eritrea or Ethiopia. Such arrivals in Somaliland would augment the locally produced Long Rains generation and participate in the Short Rains breeding in this area between October and January. Thus the intensity of monsoon breeding in southern Arabia and of Short Rains breeding in the northern Somali peninsula may be to some extent dependent on migrations across the Gulf of Aden. The July 1945 records suggest the possibility of swarms of the Arabian Spring generation reaching the Mijertein by overflying the south-west monsoon, but it is probable that many of the swarms reported as landing on the Somali coasts at this season are of local origin.

It appears probable that phase *solitaria* may exist in the northern Somalia peninsula between outbreaks, and that conditions in the coastal areas may sometimes favour the building up of large *solitaria* populations and possibly even transformation into phase *gregaria*. Thus an examination of records of locust breeding in British Somaliland during the recent outbreak, and of the corresponding climatic data, together with some preliminary observations on the vegetation of the coastal areas, have demonstrated points of similarity between western British Somaliland and known outbreak areas (Waloff & Rainey, 1948). The weather conditions concerned in the migration of swarms between Arabia and the Somali peninsula may also make possible a similar migration of phases *solitaria* and *transiens*, which, as has been demonstrated by Rao (1942) in north-west India, are capable of migrating over long distances. The coastal areas of the Somali peninsula may thus be linked with the suspected outbreak areas of south-western Arabia, and through them with the known outbreak areas on the African coast of the Red Sea, and may thus contribute to, and receive emigrants from, the *solitaria* and *transiens* populations of these areas.

Considering locust migration in general, the observed displacement of a flying swarm is given by the resultant of the movement of the locusts with respect to the air and that of the air with respect to the ground. The latter can be estimated in the form of a trajectory from the routine upper-wind observations of synoptic meteorology, while the recorded values of locust air-speed provide an approximate estimate of the magnitude of the former. The 'course' or orientation of the flying locusts is also needed to define their movement completely, but is determined by factors which are so far almost completely unknown. However, the foregoing examples demonstrate that the wind-speed concerned is frequently considerably greater than the air-

speed of the locusts, so that when a flying swarm is reported at a given time and place, the range of possible positions at any previous or subsequent time, so long as it remains airborne but considering all possible courses, may still lie within a relatively restricted area. When much of the area so defined is sea (which also satisfies the condition that the locusts should remain airborne), the possible area of origin (or destination) is narrowed down still further, as in the case of the Berbera swarm of 14 December 1945, and in favourable circumstances may be defined with certainty by consideration of other swarm records over the same period.

Swarm reports rarely record time of day, and it is therefore usually necessary to decide upon the most appropriate time at which to begin the construction of a trajectory; it may sometimes be necessary to construct several trajectories to investigate alternative possibilities. However, when the variation of the wind in the course of the day is large enough seriously to affect the resulting trajectories, as during the south-west monsoon, it is usually possible to narrow down considerably the period during which the observed swarm movement would have been possible—swarms cannot, for example, fly ashore during an offshore gale. While in such cases it is not possible to define the area of origin or destination of the swarm as rigorously as if the time of day had been recorded, the trajectory alone may throw considerable light on possible routes, as illustrated above.

On the rare occasions when records from two successive points are known to refer to the same swarm movement, the method illustrated may be used to provide information on the course or orientation maintained during the flight. No such observations are available for the Gulf of Aden area, but the movement of *Schistocerca* swarms from south-west Morocco to Portugal on 11–12 October 1945, reported by Waloff (1946*a*), may be used as an example. Thus the swarms which were off Agadir at 09.00 hr. on the 11th would have made a landfall in the vicinity of Cadiz had they maintained a constant easterly course, at right angles to the southerly wind over the sea. No locusts were actually reported anywhere east or south of the Tagus, and the recorded distribution of the locusts in relation to the corresponding trajectory indicates that the swarms reported in Portugal could not have maintained a steady course differing by more than 10° from the wind direction during the flight. Furthermore, it is unnecessary to assume that a constant orientation was maintained at all, since the observed distribution of locusts in Portugal could also have resulted from either continuous circling or frequent random changes of course. A swarm flying directly down-wind would of course have made good a higher ground-speed than one which was circling or changing course at random, and would have covered the 612 miles from Tiznit to Lisbon in 15 hr. as against the 20 required by the latter behaviour; unfortunately this difference is too small to decide between these two alternatives on the data available. Circling is however a form of swarm movement which is not infrequently reported (e.g. near Tiznit on 10 October 1945, and off Berbera on 14 December 1945), and which may easily be overlooked by a stationary observer in winds higher than the air-speed of the locusts.

The major trends of *Schistocerca* migrations in East Africa are, with some exceptions, down the prevailing winds, and change with them (Waloff, 1946*b*), and the data discussed above for landings on the Somali coasts during the south-west monsoon indicate that at least some of the apparent exceptions may also represent down-wind displacements. Such down-wind displacement, of course, does not necessarily imply down-wind orientation of flying locusts, and would in fact occur even in the complete absence of any persistent orientation.

A further point of general interest emerging from the meteorological data examined is the evidence of the significance of convection currents in relation to flying locusts, provided by the Bulhar aircraft report (p. 109), indicating convection currents up to the level of high-flying locusts, and by the association of swarm movements with rising sand, dust-storms and similar manifestations of intense convective activity near the ground. Thus each of the two reports of swarms on the east coast of the Mijertein during June 1944 refers to a day following a record of rising sand with a visibility of 2½ miles or less at Iskushuban; there were altogether four such days during the month. Again, rising sand was recorded during June 1946 at Bander Kassim on two days, each of which was followed by a day on which swarms were reported somewhere on the coast between Karin and Kandala; there was only one other day during the month on which such swarms were reported. Considering only these two sets of data, the probability of such a series of coincidences arising by chance is less than 0·0001; and further similar cases are recorded above.

Convection currents over the land may thus provide the initial height for crossings of the Gulf of Aden, and during the north-east monsoon there is also active convection over the sea at night. However, upper air temperature observations in this area (Frith, 1943; Meteorological Office, 1944) indicate the general absence of such currents over the Gulf during the south-west monsoon, when the air at 1000–2000 ft. is warmer than that at the surface, while the latter is again warmer than the sea. Such an 'inversion' or increase of temperature with height inhibits vertical air movements, so that a swarm flying above an inversion could only maintain height by muscular effort.

5. SUMMARY

1. The meteorological data relating to a number of swarm movements recorded in the Gulf of Aden area between 1941 and 1947 have been examined, using the corresponding synoptic charts.

2. The trajectory of the air in which a flying swarm is observed, considered in relation to recent determinations of the air-speed of *Schistocerca*, is shown to provide evidence of the origin and destination of the swarm, affording in favourable circumstances a good indication of its probable track, and making possible some deductions as to the course or orientation of the locusts.

3. Trajectories relating to swarms arriving on the coast of British Somaliland during the winter indicate the migration of swarms of the Monsoon generation across the Gulf of Aden from the Hadhramaut.

4. Records of swarms reaching Aden and the adjacent coast in summer give trajectories indicating the migration of swarms of the Long Rains generation from western British Somaliland, also across the Gulf.

5. It appears probable that locusts of the phases *transiens* and *solitaria* may similarly migrate across the Gulf.

6. Swarms landing on the coasts of the Somali peninsula during the summer are shown to be probably mainly of local origin, swept out to sea by the monsoon and subsequently brought in again by the sea-breeze. An alternative possibility in some of these cases is that of transportation across the Gulf by the north-easterlies which overlie the south-west monsoon and are probably continuous with the surface north-westerlies of Arabia at this season.

7. Evidence of the significance of convection currents in relation to flying locusts is provided by the frequent association of swarm movements with rising sand, dust-storms and similar manifestations of intense convective activity near the ground, and by an aircraft report of locusts at 7000 ft. at an air temperature indicating unimpeded convection currents from the surface to at least this height.

6. ACKNOWLEDGEMENTS

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ECOLOGICAL ISOLATION IN A RICH TROPICAL AVIFAUNA

By R. E. MOREAU, *Edward Grey Institute, Department of Zoological Field Studies, University of Oxford*

1. INTRODUCTION

Lack (1944) has pointed out the extent to which congeneric species of the British passerine birds are ecologically isolated. He concludes that isolation is more or less secured between most of them (*a*) geographically (3 cases); (*b*) by difference in habitat (18); (*c*) by difference in feeding zone in the same general habitat (3); (*d*) by difference in food habits (1); (*e*) by difference in size (of beak as well as of body), which presumes more or less marked difference in food taken; (*f*) by difference in winter range. There is 'apparent ecological overlap' in only '5–7 cases'.

In general, there has been increasing acceptance of the thesis of Gause (1934) that two related species that are ecologically similar cannot flourish together (cf. Crombie, 1947).

Elton (1946), on analysing a number of ecological communities, which included only a few birds, finds confirmation of 'the general proposition that some (though not necessarily all) genera of the same consumer level that are capable of living in a particular habitat at all can coexist permanently on an area; whereas it is unusual, in the communities analysed, for species of the same genus to coexist there'. Williams (1947) has concluded, as a result of mathematical investigations, that intra-generic competition is not of overriding importance in determining the composition of a community and that in fact 'in a small or simple community' selection is 'in favour of more than one species in the same genus rather than in favour of single species in single genera'. It is obvious, and has been recognized, that in discussions of this nature much turns upon the breadth of the concept of both the genus, and the community, that is adopted. In fact Williams's conception of a 'community' for this purpose is exceedingly broad.

It appears that a useful contribution to the discussion can be derived from analysis of a local avifauna so rich in species that it is possible to compare the prevalence of ecological isolation both between congeneric species and between species that belong to the same family but are not congeneric.

I am indebted to David Lack for both the original inspiration of this paper and for help in arranging the data.

A suitable avifauna for the present purpose is that of Usambara, Tanganyika Territory, where in an area of 3000 sq. miles (about the size of Kent plus Surrey) some 400 species of birds breed. For the present purpose the boundaries used are those of a parallelogram with corners at approximately 4° 30′ S. by 38° E., 5° S. by 38° E., and 5° and 5° 30′ S. on the shore of the Indian Ocean. (See maps in Sclater & Moreau, 1932, facing p. 522; and Moreau, 1935*a*, p. 3.) These boundaries include altitudes from sea level to nearly 8000 ft., with some localities on the seaward side that average 80 in. of rain a year and others in the 'rain-shadow' inland that get 20 in. of rain in a good year and 5 in. in a bad. The result is that a number of strikingly different vegetation types and habitats are crowded into a relatively small area. Moreover, for the present purpose Usambara has the advantage over most Western Palaearctic areas that a good proportion of the land surface is in a 'natural' condition, though not so large a proportion as in some parts of Africa.

The economy of individual species is naturally not so exactly known as in a European area, but Usambara is, for a tropical area, comparatively well documented, and during many years I have studied birds there in collaboration with my wife. Most of the species found there were listed with field notes by Sclater & Moreau (1932–3) though a number have been added since (Moreau, partly unpublished). A general syn-ecological outline of Usambara has been given, in which the various bird communities were listed on the background of climate and vegetation; and some problems of the local distribution of the birds were subsequently discussed (Moreau, 1935*a*, *b*).

Apart from the Falconidae, the ecology of which I know too imperfectly to use for the present purpose, the largest families of birds in Usambara and those which provide the material for the present study, are the barbets (Capitonidae), 11 species; bulbuls (Pycnonotidae), 15 species; flycatchers (Muscicapidae *sensu stricto*), 18 species; thrushes (Turdidae), 20 species; 'warblers' (Sylviidae), 28 species; shrikes (Prionopidae and Laniidae), 21 species; sunbirds (Nectariniidae), 17 species; weavers (Ploceidae), subfamilies Ploceinae and Estrildinae, 21 species each.

It is important that analysis and discussion should be by family as well as by genus, because, as has increasingly been recognized, 'the genus of the systematist is his own artificial creation and not a natural unit'. This *caveat* is nowhere more necessary than in dealing with African birds, which have by South

African workers been subjected to extreme genus-splitting and have at the other extreme undergone extensive genus-'lumping', with multiplication of subgenera, in recent revisions made in the U.S.A. The classification followed in this paper is that of Sclater's *Systema Avium Aethiopicarum*, which represents a middle course. The generic distribution of the species dealt with in this present paper is shown in Table 1.

For the present purpose the zones, main habitats* and subdivisions shown in Table 2 are used, giving a total of 32 subdivisions. It will be seen that the different 'feeding zones in the same general habitat' are ranked as subdivisions, a procedure that seems fully justified.

The Usambara forests are exceptionally tall and luxuriant, especially in the intermediate zone. The trees there reach a height of 150 ft.: the light intensity in the ground stratum does not exceed 1% of that outside the forest. Consequently, the vertical divisions of the Rain Forest, tree-tops, mid-stratum and ground stratum, although part of one main habitat, are virtually separate habitats. Birds allocated to the 'ground stratum' are those which feed on the ground or in the lowest few feet of the undergrowth. Nearly all of them nest in the undergrowth, not on the ground, but in the same layer of vegetation as many of the birds allocated to the 'mid-stratum'; but the latter forage upwards, through the tops. The importance of the fourth subdivision, the 'edges', of the Rain Forest has been stressed elsewhere (Moreau, 1935*b*). The term is not intended to be restricted to the external edges of forest area, but to include also the edges of all openings, the most important of which are along streams. The 'edges' can practically be said to have a peculiar fauna.

* The terms 'Parkland' and 'Savannah' used in former descriptions have been replaced by 'Grassland' (with trees) in agreement with a vegetation classification for eastern Africa that is in preparation.

2. THE USAMBARA DATA

In the Appendix each of the 172 species comprised in the nine families dealt with is allocated to its habitat subdivision(s), primarily with reference to its feeding range. (In the species concerned competition† for nest-site is probably not significant.) The allocation that is correct in Usambara is not necessarily so in other localities. In fact, the proximity of the area to the Indian Ocean and its peculiar topography, with consequent peculiar climate, produce abnormal combinations of altitude and habitat. In general, the birds dealt with are closely restricted to the habitat subdivisions specified for each of them; and it may be especially emphasized that the ecological separation between rain-forest and non-rain-forest birds is as a rule absolute.

Where in the Appendix any two species are allocated to the same habitat subdivision they are classified as providing a case of habitat overlap. At the end of each family these cases are summarized and any available information is adduced to suggest whether the constituent species have a mainly different diet. (In the absence of definite information, marked difference in size of beak and of body is provisionally accepted as presumptive evidence of significant difference in diet.) If there is no indication of difference in diet between any two species in the same habitat subdivision, their case is classified as one of 'apparent ecological overlap', the application of this term thus being dependent on two criteria. This does not necessarily mean that two such overlapping species are in competition, since the food on which both of them appear to depend may in fact be more than enough for both of them.

Table 3 summarizes the results of this analysis. Each species in a family is theoretically capable of

† Defined as 'the demand at the same time by more than one organism for the same resources of the environment in excess of immediate supply' (Crombie, 1947).

Table 1. *Distribution of Usambara birds between genera*

Family	Number of genera having									
	1 sp.	2 spp.	3 spp.	4 spp.	5 spp.	6 spp.	7 spp.	8 spp.	9 spp.	10 spp.
Capitonidae	2	3	1	—	—	—	—	—	—	—
Pycnonotidae	3	1	1	—	—	—	1	—	—	—
Muscicapidae	7	4	1	—	—			—	—	—
Turdidae	7	2	3	—	—	—				—
Sylviidae	10	3	—	—	—	2	—	—	—	—
Prionopidae and Laniidae	8	5	1	—	—	—	—	—	—	—
Nectariniidae	2	1	1	1	—	1	—	—	—	—
Ploceidae:										
Ploceinae	3	2	—	1	—	—	—	—	—	1
Estrildinae	9	3	2	—	—	—	—	—	—	—
Total	51	24	10	2	—	3	1	—	—	1

Table 2. *Habitats*

Zone	Main type	Subdivision
1. Lowland, 0–2500 ft.	*a.* Rain Forest	(1) Tree-tops (2) Mid-stratum (3) Ground stratum (4) Edges
	b. Riverine Forest (often reduced to the merest fringe)	(1) Trees (2) Ground stratum
	c. Wooded grassland—grass of upright habit with scattered trees and clumps of semi-evergreen bush. A pyrophytic climax (annually swept by 'bush fires')	(1) Grass (2) Trees (deciduous) (3) Low semi-evergreen bush (4) Tall clumps of semi-evergreen bush
	d. Semi-desert vegetation ('Thorn Country'). Various densities of tree-growth (most under 15 ft. high) almost entirely deciduous and thorny. A few small semi-evergreen bushes and trees. Annual herbage locally covers the ground, but soil bare (not because of fires) much of the year	(1) Trees and bushes (2) Ground (including woody herbage) (3) Riverine strips
	e. Induced vegetation types. Cultivation of various crops, mostly associated with rank grass and herbage and regenerating bush	(1) Trees and tall bushes (2) Dense low bush (3) Herbaceous cover (4) Scantily covered ground, especially under coco-palms and about villages
	f. Swamp	
2. Intermediate, 2500–4500 ft.	*a.* Rain Forest	(1) Tree-tops (2) Mid-stratum (3) Ground stratum (4) Edges
	b. Grassland—rank upright grass with occasional woody herbs and small trees	
	c. Induced vegetation (forest clearings)	(1) In East Usambaras (humid), largely occupied with rank herbage, procumbent grass and regenerating bush (2) In West Usambaras (semi-humid), associated with short grass (turf) and woody herbage
3. Highland, 4500–7500 ft.	*a.* Rain Forest	(1) Tree-tops (2) Mid-stratum (3) Ground stratum (4) Edges
	b. Moorland (with much evergreen bush up to about 5 ft.)	
	c. Induced vegetation (mainly cultivation associated with short grass and woody herbage)	

producing a case of habitat overlap with every other species of that family and the figures in columns 3 and 5 are calculated on the number of possible combinations of two species. Columns 4 and 6 show the number of cases in which two members of the same family are in fact found feeding in the same habitat subdivision. Even on our present exceedingly imperfect knowledge, there is reason to believe that a large proportion of those species which occur together are ecologically separated by differences in diet. The residue of species that appear to provide cases of actual ecological overlap are given in columns 7 and 8 of Table 3. But even of these a large proportion are qualified by the fact that one or both members of the pair are rare, or that the geographical overlap between them in Usambara is limited. The number of cases of ecological overlap which are so qualified is shown in columns 7 and 8 in brackets.

theoretically possible; and in view of the imperfect knowledge of the species' ecology, which I must lose no opportunity to emphasize, the difference between the two groups is doubtfully significant. But there is no likelihood that additions to knowledge will upset the main conclusion, namely, that the prevalence of unqualified ecological overlap is remarkably low both in congeneric species and in others.

The means by which so high a degree of ecological isolation is brought about between species that live in the same habitat are practically in all cases ascribable, as will be seen from the Appendix, to differences in size (of beak or body, with differences in diet usually presumed but rarely known) or to differences in foraging methods (or foraging range) within the habitat subdivision. Occasionally both factors are perceptible in the same cases of habitat overlap. The

Table 3. *Habitat overlap and ecological overlap in Usambara birds*

		No. of cases of habitat overlap				No. of cases of apparent ecological overlap	
		Within genera		Others			
Family	No. of species	Possible	Actual	Possible	Actual	Within genera	Others
(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)
Capitonidae	11	6	2	49	5	2 (1)	None
Pycnonotidae	15	24	7	81	4	2 (1)	None
Muscicapidae	18	7	None	146	19	None	2 (2)
Turdidae	20	11	2	179	21	None	8 (6)
Sylviidae	28	33	5	345	19	2	9 (3)
Prionopidae and Laniidae	21	8	None	202	20	None	3 (3)
Nectariniidae	17	25	2	111	10	1	1
Total	130	114	18 (15·8 %)	1113	98 (8·8 %)	7 (2)	23 (14)
Ploceidae:							
Ploceinae	21	53	17	157	60	13 (2)	40 (8)
Estrildinae	21	6	None	204	21	None	16

It is at once obvious that the weavers, especially the Ploceinae, present a different ecological picture from all the other groups dealt with in this study and they will be discussed separately below. Excluding the Ploceidae, Table 3 shows that out of 114 theoretically possible cases of habitat overlap between congeneric species, only 18 (16 %) actually occur, and of these only seven (about one-third) appear to overlap ecologically. Moreover of these seven only five are unqualified. Corresponding figures for species that are not congeneric are 1113, 98 (9 %) and 23 (nine unqualified). These results would indicate that habitat overlap and apparent ecological overlap are both actually more prevalent between congeneric species than between species that are not so closely related. The numbers of cases involved are, however, in both groups only a small percentage of those

prevalence of these two means of isolation is shown for each family in Table 4. In arriving at the 'points' for each means of isolation half a point has been awarded to each in cases where both seem operable.

The Ploceinae differ from all the other groups in that as many as 11 species of them occur together in the breeding season in areas where there is plenty of food, above all in deflooded riverine strips that are partly under rice cultivation and partly under heavily seeding grasses. Some of these weavers nest in reeds and bulrushes, others in rank grass, others in neighbouring trees; but there seems no doubt that all draw mainly on the temporarily enormous amount of food (seed)—presumably 'superabundant' in the sense of Lack (1946)—that is utilized by them in common. As the dry season progresses, this teeming bird population begins to disappear. At first certain

of them, especially the *Quelea* spp., maintain themselves mainly by foraging outside the riverine strip, on seeds of the ephemeral vegetation in the surrounding semi-desert area (where at this season they must to some extent compete with the smaller, Estrildine, weavers resident there). It is for this reason that in column 8 of Table 3, eight of the 40 cases of ecological overlap in the Ploceinae are bracketed as 'qualified'. Ultimately nearly the whole of the Ploceine population of the riverine strip disappears until the next rains. We do not know where the birds go and, since there is no indication that those of any species go beyond the limits of the breeding range of that species, their off-season movements will take a long time to elucidate. However, there is little doubt that they must seek localities in which a different incidence of rainfall or of floodwater has induced a supply of seed at a season different from that in Usambara; and there is no reason to think that the ecological overlap that is so pronounced during the breeding season is absent in 'winter' quarters.

The foregoing remarks about the riverine strip in semi-desert country apply with much the same force to the Ploceine population of the better-watered country between the mountains and the sea. Although this area enjoys two rainy seasons in the year, the intervening periods witness a very marked reduction in supply of grass, 'weed' and crop seeds, and a corresponding redistribution of the Ploceine population.

The other Ploceid subfamily here dealt with, the Estrildinae, with the same number of species in Usambara as the Ploceinae, but with nearly three times the number of genera, makes a different showing in Table 3 and is more like the non-Ploceid groups. A somewhat greater extent of overlap is, however, evident even in the Estrildinae; and this applies not only to those species which depend upon, and share, the temporary abundance supplied by the ephemeral vegetation of the semi-desert, but also by those which live in the evergreen clearings of the East Usambara Mountains. *Coccopygia*, *Estrilda* and *Spermestes* may there constantly be seen feeding on the same grasses (*Panicum* spp.).

The general results of analysing the Usambara data given in the Appendix may be summarized as follows:

(*a*) It is unusual, but not rare, for congeneric species to coexist in the same habitat subdivision; and it is actually more unusual for species to do so that are not congeneric (but belong to the same family).

(*b*) It follows that, at least on the system of classification here used, the generic level of relationship is of no particular importance for the problem under discussion, and consequently that intra-generic relationship is not of overriding importance in determining the composition of a community.

(*c*) The fact is, however, that most of the cases of habitat overlap apparently do not involve overlap in diet and hence are not cases of complete ecological overlap and do not involve competition.

(*d*) The low percentages of ecological overlap show that the forces operating to avoid it are very effective. In this connexion it is worth while to consider two phenomena of which Africa provides notable examples, namely the replacement of one locally absent species by another and the foraging by several species in association.

Table 4. *Cases of habitat overlap in which there does not appear to be ecological overlap*

	Presumptive means of isolation			
	Difference in size		Difference in foraging methods within habitat	
Family	Within genus	Different genera	Within genus	Different genera
Capitonidae	—	5	—	—
Pycnonotidae	2	—	3	—
Muscicapidae	—	6	—	11
Turdidae	1	7	1	6
Sylviidae	3	4	—	6
Prionopidae and Laniidae	—	6	—	11
Nectariniidae	—	8	1	1
Total	6	36	5	35
Ploceidae:				
Ploceinae	3	3	1	17
Estrildinae	—	5	—	—

3. SOME CASES OF ECOLOGICAL REPLACEMENT

Montane evergreen forest in East Africa forms a large number of well-separated ecological islands. In some of them a characteristic member of the montane

forest bird community is absent and its niche is occupied by a species from a different community. This may indicate that such species, having closely comparable needs, tend to be mutually exclusive. And it will be seen that the examples consist not only of congeneric species but also of less closely related members of the same family.

The cases mentioned below are of the more interest because most of them involve species on the Usambara list (for which habitats have been defined in the Appendix). It will be noticed that most of the instances are drawn from the Highland Forests of the Mbulu District of Tanganyika Territory (see map facing p. 760, in Moreau, 1937), but no reason can be suggested why these forests should be so marked a focus of ecological abnormality.

Capitonidae

(1) Nearly all the montane forests of eastern Africa from Kenya southwards are occupied by one or both of the little barbets, *Pogoniulus bilineatus* and *Viridibucco leucomystax*. On Hanang Mountain, where both these species are missing, *Pogoniulus pusillus*, normally a bird of deciduous trees at lower altitudes, appears in the mountain forests (Fuggles-Couchman, unpublished). (But this does not happen in the neighbouring forests of the Mbulu District, where the fruit-eating barbets are not represented at all.)

(2) *Buccanodon olivaceum* is in Usambara a bird of Lowland and Intermediate Rain Forest, where it seems to be in complete ecological overlap with *B. leucotis*. In the Highland Rain Forest of Usambara (and of Kilimanjaro) only the latter species occurs. In the Poroto and other mountains round the head of Lake Nyasa *B. leucotis* has not been found; but there, and apparently only there, *B. olivaceum* occupies Highland Forest. This presumably means that the two species can coexist indefinitely in Lowland and Intermediate Forest—perhaps because the fruits that form the food are relatively abundant—but that *B. leucotis* is better adapted than *B. olivaceum* to life in the highlands.

Picidae

It appears that no montane forest in eastern Africa includes in its bird community more than one species of woodpecker. This is the more surprising since the ratio of bark-surface to unit of ground-area is very great and specialization of woodpeckers for different types of wood feeding might well be facilitated. (Compare the European woodlands, where the weak-billed *Dendrocopos medius* lives alongside stronger-billed species and depends on insects that can be obtained without boring in hard wood (Voous, 1947).)

The most northerly East African forests, those of Abyssinia, are occupied by a *Dendropicos* (*D. abyssinicus*), those of Kenya by a *Campethera* (*C. taeniolaema*) and those farther south by a *Mesopicos* (*M. griseocephalus*). In one area, Mbulu, contiguous to the ranges of both the *Campethera* and the *Mesopicos*, both are missing, and the forests are occupied by a peculiarly dark form of *Yungipicus obsoletus*, a species that everywhere else belongs to scattered deciduous trees in semi-arid country. This particular substitution is the more remarkable because another member of the genus *Mesopicos* (*M. rhodeogaster*), lives in acacia woods close to the Mbulu forests and has presumably been 'available'.

Muscicapidae

Trochocercus species occupy most of the forests of eastern Africa, *T. albonotatus* being everywhere a bird of Highland and Intermediate Forests, *T. cyanomelas* mostly of Intermediate and Lowland. Apparently they are nowhere members of the same forest community. In Usambara *T. albonotatus* occupies the forests down to about 3000 ft., *T. cyanomelas bivittatus* the forests below that. Again, in Kenya, *T. cyanomelas kikuyuensis*, which differs from *T. c. bivittatus* only by being larger, occupies the lower part of the Kenya Highlands, e.g. round Nairobi, which is below the range of *T. albonotatus*.

This latter species is inexplicably absent from a number of apparently suitable high-altitude forests that are within its geographical range. In the Mbulu District forests and also in those of the Chyulu Mountains (van Someren, 1939) the place of *T. albonotatus* is taken by *T. cyanomelas bivittatus* (the lowland form, not the larger *T. c. kikuyuensis* that would have been more likely); on Kungwe Mountain in western Tanganyika by *T. cyanomelas vivax*; and on Nchisi Mountain in Nyasaland by a very different bird, of another genus, *Tchitrea plumbeiceps*, a paradise flycatcher that is not normally a rain-forest bird at all (Benson, unpublished).

It may be added that *Trochocercus albonotatus* is absent also from Kilimanjaro, but seems on that mountain to have no substitute.

Sylviidae

Most of the East African mountain forests are occupied by *Sathrocercus mariae*, with *S. cinnamomeus* living in heath and other evergreen scrubby vegetation in immediate proximity to the forests. On Hanang Mountain (Mbulu District), where *S. mariae* is absent, *S. cinnamomeus* takes its place in the forest community (Fuggles-Couchman, unpublished).

Turdidae

In Abyssinia, Kenya and northern Tanganyika *Cossypha semirufa* occupies the Highland Forests (down to about 5500 ft.) and up to about 6000 ft.; *C. heuglini*, a lowland species, occurs in low, dense more-or-less evergreen bush outside. In the Mbulu

District forests *C. semirufa* is absent and the other species takes its place.

PLOCEIDAE

Low-altitude forests in coastal East Africa and western Tanganyika are occupied by insectivorous weavers of the *Symplectes* group, higher forests in Kenya and western Tanganyika by *Ploceus* (*Phormoplectes*) *insignis*. But in the Highland Forests of Oldeani and Hanang, where the above species are absent, their niche is occupied by (undifferentiated) birds of the species *Ploceus* (*Hyphanturgus*) *brachypterus*, which elsewhere lives in low, more-or-less evergreen bush in the Lowland and Intermediate zones. (Apparently on Kilimanjaro, as on the mountains of southern Tanganyika and of Masailand, no Ploceid is a member of the forest community.)

4. MIXED FORAGING PARTIES

Mixed foraging parties of insect-eating birds are exceptionally well developed in the tropical African biota that are well supplied with trees; and they so often contain closely related species that they are worthy of special study in connexion with the present inquiry. The most careful description of the interrelations in such parties has been provided by Swynnerton (1915), while Stresemann (1917) has published a more general review. There seems no doubt that the members of these parties derive benefit from each others' activities and it is probable that there is at the same time a specialization in food capture.

I am familiar with mixed parties in both the *Acacia—Commiphora* 'thorn country' and the Rain Forests of Usambara, but unfortunately I have been able to do little more than record components. A few examples will suffice; and an interesting feature of some of them is that birds not normally insectivorous occasionally join foraging parties. For example:

In 'thorn country'

(1) A woodpecker (*Campethera*), two wood-hoopoes (*Rhinopomastus*)—with a long, 'prying' beak, not an awl like a woodpecker's—several 'warblers' (both *Eremomela* and *Sylvietta*), and a tit-babbler (*Parisoma*).

(2) A thrush (*Turdus*) working the ground, several 'warblers' (*Apalis* and the longer-beaked *Sylvietta*), two white-eyes (*Zosterops senegalensis*), three *Gymnoris pyrgita* (misnamed 'rock sparrows') and a pair of cordon bleus (Estrildine weavers, *Uraeginthus*).

In these parties it may be assumed that the woodpecker and the wood-hoopoe, with their different equipment, are largely complementary. In the absence of evidence *Parisoma*, *Zosterops*, the warblers and *Gymnoris* (a largely insectivorous sparrow) would be regarded as probably eating much the same food as the 'warblers'. *Uraeginthus*, a typically seed-eating species, is a surprising addition. I have, however, seen it pecking open termite-runs up tree-trunks and in this particular party *Uraeginthus* might benefit by the activities of the woodpecker and the wood-hoopoe—though practically this would mean competition with them.

In Rain Forest

(1) One to about a dozen individuals of each of the following: woodpecker (*Dendropicos*), a little honeyguide (*Prodotiscus*), two bulbuls (*Phyllastrephus fischeri* and *P. flavostriatus*), two flycatchers (*Batis* and *Trochocercus*), two 'warblers' (*Camaroptera* and *Apalis*), a shrike (*Sigmodus*), a drongo (*Dicrurus*), a cuckoo-shrike (*Coracina*) and a weaver (*Ploceus*).

In each of the two families and one genus that had two species present there was no ecological overlap. One of the *Phyllastrephus* spp. and one of the 'warblers' consistently foraged at a lower level in the vegetation than the other species of the same genus; and of the two flycatchers one feeds more on the wing than the other. One would, however, expect a good deal of overlap to take place between the last four species on the list. The appearance of *Prodotiscus* is unexpected since its staple is scale-insects, a prey that would not seem to be brought to notice particularly by the foraging party.

(2) Representatives of one bulbul (*Phyllastrephus*), two flycatchers (*Alseonax cinereus* and the very small *Chloropetella*), a warbler (*Apalis*), a drongo (*Dicrurus*), three sunbirds (*Anthreptes neglectus*, *A. yokanae* and *A. collaris*) and a weaver (*Ploceus*).

The occurrence of the three sunbirds is of particular interest; they all belong to the relatively unspecialized genus *Anthreptes*, the members of which depend little on flower juices and somewhat on minute fruits as well as insects.

The appearance of two or more members of a genus in the same foraging party has frequently been recorded, e.g. two *Dicrurus* spp. in Bali, two *Pachycephala* spp. and two *Rhipidura* spp. in Seran (Stresemann, 1917). Chapin (1932, pp. 221–2) cites five bulbuls, including two *Phyllastrephus* spp. and two *Bleda* spp., two *Alethe* spp., two *Illadopsis* spp., several flycatchers including two *Tchitrea* spp. and two *Diaphorophyia* spp., two *Malimbus* spp. and two *Nicator* spp. It is not clear to what extent these pairs of species actually occur together in the same party; but from the point of view of the present inquiry it is important that all reports of congeneric species in foraging parties should be analysed. It at least seems certain that the presence of two *Phyllastrephus* spp. is a regular feature of African forest parties. Nearly 1500 miles south of Usambara Swynnerton (1915) found *P. terrestris* (*P. capensis* of many authors) and

P. flavostriatus foraging one below the other just like *P. fischeri* and *P. flavostriatus* in the north.

SUMMARY

1. In a tropical African area of about 3000 sq. miles, nine families of birds are represented by 172 species in 92 genera, 41 of which show more than one species. Considered family by family these birds provide in all 173 cases of theoretically possible ecological overlap between species of the same genus and 1474 cases between other species.

2. Thirty-one habitat subdivisions are adopted and each species is allocated to the subdivisions in which it forages. The Ploceidae (weavers) present a different ecological picture from the other families (which are frugivorous and insectivorous).

3. Excluding the Ploceidae, within genera only 16% of the theoretically possible cases of habitat overlap are realized and in only one-third of these is there apparent overlap in diet and consequently ecological overlap. Moreover, some of the 'cases' are qualified by the fact that one or both the species concerned are present in such small numbers that 'competition' is unlikely.

4. Of the congeneric species 94% are ecologically isolated from each other, since they are distinct in habitat or in diet or in both. The corresponding figure for the other species in the same families is 98%. It follows that the isolating mechanism is at least as effective between the non-congeneric species as between the congeneric; and it may provisionally be inferred that generic relationship is not of overriding importance in determining the composition of a community.

5. The grounds for concluding that most of the cases of habitat overlap are not cases of diet overlap (and consequently not cases of ecological overlap) are almost entirely (1) differences in size (of body or beak), and (2) differences in details of food-seeking methods or of range within the habitat. These two means of ecological separation are about equally prevalent.

6. Among the Ploceidae, which have been excepted from the foregoing remarks, the subfamily Ploceinae shows a much higher percentage of both habitat overlap and ecological overlap than either the other Ploceid subfamily, the Estrildinae, or the non-Ploceid families. This result is due to the fact that numerous Ploceine species feed together on the temporarily superabundant graminaceous food produced in, for example, flood-plains. As the dry season progresses and the seed supply disappears, so do the Ploceinae that have been feeding on it. It seems likely that they move from one focus of temporary superabundance to another.

7. Mixed foraging parties, so prominent in Africa, often contain more than one species of the same family or the same genus. Preliminary indications are that in these cases the respective foraging habits are complementary.

8. The inference from the foregoing is that the forces that minimize ecological overlap between related birds are highly effective. This derives confirmation from a number of cases cited where a widespread African species is, in one or more localities, inexplicably absent from its niche. Its place is then often taken by another species of the same family, sometimes of the same genus, and usually, but not always, from the same biome.

APPENDIX

Habitat allocations (for code numbers see Table 2)

Capitonidae

A 1 *Lybius torquatus irroratus*: 1 *c*(2).
A 2 *L. melanopterus*: 1 *b*(1).
B *Tricholaema melanocephalum stigmatothorax*: 1 *d*(1).
C 1 *Buccanodon leucotis kilimense*: 1 *a*(1), 2 *a*(1), 3 *a*(1).
C 2 *B. olivaceum olivaceum*: 1 *a*(1), 2 *a*(1).
D *Viridibucco simplex. V. s. simplex*: 1 *a*(1); *V. s. leucomystax* 2 *a*(1), 3 *a*(1).
E 1 *Pogoniulus pusillus affinis*: 1 *c*(2).
E 2 (*P. bilineatus fischeri*: 1 *a*(1). From its distribution just outside our limits this bird is virtually certain to occur in the tree tops of the Lowland Forest on the coast, but it has not actually been collected within our limits.)
F 1 *Trachyphonus vailliantii suahelicus*: 2 *c*(2).
F 2 *T. e. erythrocephalus*: 1 *d*(2).
F 3 *T. d'arnaudii boehmi*: 1 *d*(2).

Analysis of cases of habitat overlap

(1) Within genera:

C 1 and C 2. These two *Buccanodon* spp. appear to provide a case of unqualified overlap in the tree tops of the Lowland and Intermediate Forest. Geographically and altitudinally in Usambara the range of *B. olivaceum* is contained in that of *B. leucotis*; there is no difference in size, in strength of beak, or apparently in food.

F 2 and F 3. These *Trachyphonus* spp. do not seem to be separated ecologically but to a great extent they are geographically. *T. erythrocephalus* is a northern species, *T. d'arnaudii* a southern; they overlap in part of northern Tanganyika Territory, including extreme western Usambara, where *T. d'arnaudii* is much the commoner.

(2) Between members of different genera: A 1 and E 1, C 1 and D, C 2 and D, C 1 and E 2, C 2 and E 2. In each of these pairs the first is much the bigger bird.

PYCNONOTIDAE

A *Pycnonotus xanthopygos micrus*: 1*c*(1), 1*e*(1), 2*c*(1), 3*c*(2)—trees in cultivation and clearings in all zones; also in Lowland Grassland (with trees), from which the present main population centres must have been colonized.

B1 *Phyllastrephus terrestris suahelicus*: 1*b*(2).

B2 *P. s. strepitans*: 1*b*(2).

B3 *P. flavostriatus tenuirostris*: 1*a*(2), 2*a*(2).

B4 *P. debilis* subspp. *P. d. rabai*: 1*a*(3), intergrading with *P. d. albigula* 2*a*(3) and 3*a*(3).

B5 *P. fischeri* subspp. *P. f. fischeri*⇌*münzneri*: 1*a*(3). *P. f. placidus* 2*a*(3), 3*a*(3)—ground stratum, but also foraging up into mid-stratum.

B6 *P. cerviniventris*: 1*b*(2).

B7 *P. orostruthus amani*: apparently 2*a*(3) but known only from a single specimen.

C1 *Arizelocichla tephrolaema usambarae*: 3*a*(2).

C2 *A. milanjensis striifacies*: 2*a*(4), 3*a*(4)—forest edges but not close to ground.

C3 *A. masukuensis roehli*: 2*a*(2), 3*a*(2).

D *Chlorocichla flaviventris centralis*: 1*e*(2), 1*c*(4).

E *Andropadus i. insularis*: 1*c*(3).

F *Eurillas v. virens*: 1*a*(4), 2*a*(4)—forest edges, just inside and close to ground.

G *Suaheliornis k. kretschmeri*: 1*a*(4), 2*a*(4)—as *Eurillas*. Allocation to Pycnonotidae doubtful. We do not think *Suaheliornis kretschmeri* in Usambara joins mixed bird-parties (which typically work the mid-stratum), but gets its food on and close to the ground. Vincent (1935, p. 357) writing of the southern form *S. k. griseiceps* states that 'in the Netia Forest the birds were. . . invariably going in parties of five or six individuals, which spent their time scratching about among dead leaves under the thickest bushes'. (But on the following page he reproduces notes he made, also in the Netia Forest, of *Suaheliornis* in a mixed bird-party 'going over the same trees and bushes' as flycatchers, drongos and other forest birds.)

Analysis of cases of habitat overlap

(1) Within genera:

B1 and B2, B1 and B6, B2 and B6. *Phyllastrephus terrestris* and *P. strepitans* are the closest in appearance and the most widespread. Both apparently get their food on ground strewn with dead leaves. *P. strepitans* seems on the whole to favour drier vegetation, is slightly smaller and has a beak that is disproportionately smaller; but it is doubtful whether the differences are enough to indicate different feeding habits.

P. cerviniventris does not occur on the coast and in Usambara overlaps the other two very little geographically. (But near the Zambesi there is extensive overlap with *P. terrestris*, cf. Benson (1940), Vincent (1935); however, it apparently gets less of its food on the ground than the other two birds.)

B4 and B5. *P. debilis* is much the smaller.

B4 and B7. As preceding.

B5 and B7. Birds much the same size but *P. orostruthus* is exceedingly rare.

N.B. In Usambara there appears to be no habitat overlap between B3 and B5, but in Portuguese East Africa Vincent (1935, p. 364) has recorded *Phyllastrephus fischeri münzneri* (under the name *P. a. itoculo*) as 'more often than not moving along with' *P. flavostriatus* 'in search of food'. This indicates either direct and regular competition between these two congeneric species of about the same size or a specific restriction in (insect) diet that remains to be worked out.

C1 and C3. The former is much the bigger.

(2) Between members of different genera:

B3 and C3. The *Phyllastrephus* is predominantly an insect eater and the *Arizelocichla* a fruit eater, feeding, moreover, rather closer to the ground.

C2 and F. The *Arizelocichla* feeds at a higher level than the *Eurillas* and is also bigger.

C2 and G. The *Arizelocichla* is predominantly frugivorous, the *Suaheliornis* insectivorous.

F and G. As preceding.

MUSCICAPIDAE

A1 *Alseonax minimus murinus*: 2*a*(4), 2*c*(1), 3*a*(4). In coffee plantations as well as on the forest edge—one of the very few birds of the forest community that has adapted itself to life outside.

A2 *A. cinereus cinereola*: 1*a*(1).

B *Parisoma plumbeum orientale*: 1*a*(4).

C1 *Bradornis griseus subalaris*: 1*c*(2).

C2 *B. microrhynchus*: 1*d*(1).

D *Melaenornis pammelaina tropicalis*: 1*c*(1), 2*c*(1).

E *Chloropeta natalensis massaica*: 2*c*(1), 3*c*, especially in rank herbage.

F *Chloropetella holochlorus*: 1*a*(1), 1*a*(4).

G *Bias musicus changamwensis*: 1*c*(4), 1*e*(1).

H *Hyliota australis usambara*: 1*a*(4), 2*c*(4).

J1 *Batis mixta*: 1*a*(2), 2*a*(2).

J2 *B. molitor soror*: 1*c*(2), 2*c*(1).

J3 *B. minor suahelicus*: 1*d*(1).

K *Platysteira peltata brevipennis*: 1*b*(2), 1*e*(2).

L1 *Trochocercus b. bivittatus*: 1*a*(2).

L2 *T. a. albonotatus*: 2*a*(2), 3*a*(2).

M1 *Tchitrea perpicillata ungujaensis*: 1*a*(4), 2*a*(4).

M2 *T. viridis ferreti*: 1*c*(4), 1*e*(1).

Analysis of cases of habitat overlap

(1) Within genera: no cases of ecological overlap.

(2) Between members of different genera:

A 1 and D. The *Melaenornis* is much bigger than the *Alseonax* and frequents more open situations in the clearings.

A 1 and E. The *Alseonax* is arboreal, the *Chloropeta* is not.

A 1 and J 2. Actual ecological overlap probable but combined density of population so low that competition probably does not occur.

A 1 and M 1. The *Alseonax* is only two-thirds the size of the *Tchitrea* and it tends to feed more outside the forest edge.

A 2 and F. The *Chloropetella* is smaller than the *Alseonax* (which is not numerous).

B and F. The *Chloropetella* is only half the size of the *Parisoma*.

B and H. Both in such small numbers that there can be no effective competition.

B and M 1. The *Parisoma* frequents a higher stratum of the forest than the *Tchitrea*.

C 1 and J 2. The *Bradornis* is much bigger than the *Batis* and gets much prey on the ground.

C 2 and J 3. As preceding.

D and E. The *Melaenornis* frequents more open and taller vegetation than the *Chloropeta*.

D and J 2. The *Melaenornis* is much bigger than the *Batis*.

E and J 2. The *Batis* frequents low trees, the *Chloropeta* herbage.

F and H. The *Chloropeta* is much smaller than the *Hyliota* and is not arboreal.

F and M 1. The *Chloropetella* is smaller than the *Tchitrea* and also feeds higher.

G and M 2. The *Bias* uses exposed perches on trees, the *Tchitrea* keeps in thickly foliaged trees.

H and M 1. The *Hyliota* (which is rare) lives higher up in the forest edge than the *Tchitrea*.

J 1 and L 1. The *Batis* is a more compact bird, less well adapted for hovering flight, that apparently takes less of its food on the wing than the *Trochocercus* does.

J 1 and L 2. As preceding, with the addition that the *Trochocercus* is smaller than the *Batis*.

TURDIDAE

A 1 *Turdus libonyanus tropicalis*: 1 *e*(4).
A 2 *T. tephronotus*: 1 *d*(2).
A 3 *T. olivaceus roehli*: 2 *a*(1), 3 *a*(1).
B *Geokichla gurneyi usambarae*: 2 *a*(3), 3 *a*(3).
C *Neocossyphus r. rufus*: 1 *a*(3), 2 *a*(3).
D *Oenanthe pileata livingstonii*: 1 *d*(2).
E *Thamnolea cinnamomeiventris subrufipennis*: on rocky outcrops in zones 2 and 3.
F *Saxicola torquata axillaris*: 2 *b*(2), 3 *b*, 3 *c*.
G 1 *Cossypha heuglini intermedia*: 1 *c*(4), 1 *e*(2), 2 *c*(1), 2 *c*(2).
G 2 *C. natalensis*: 1 *a*(3).
G 3 *C. caffra iolaema*: 3 *b*, 3 *c*.
H *Sheppardia sharpei usambarae*: 2 *a*(3), 3 *a*(3).
J 1 *Alethe fülleborni usambarae*: 2 *a*(3), 3 *a*(3).
J 2 *A. montana*: 3 *a*(3).
K 1 *Cichladusa arquata*: 1 *c*(3), 1 *e*(2).
K 2 *C. guttata rufipennis*: 1 *c*(3), 1 *d*(4), 1 *e*(2).
L 1 *Erythropygia leucophrys soror*: 1 *c*(3).
L 2 *E. leucoptera leucoptera*: 1 *d*(2).
L 3 *E. q. quadrivirgata*: 1 *c*(4), 1 *e*(2).
M *Pogonocichla stellata orientalis*: 3 *a*(3) and more rarely 2 *a*(3) and 1 *a*(3).

Analysis of cases of habitat overlap

(1) Within genera:

J 1 and J 2. *Alethe fülleborni* is much bigger than *A. montana*, which, moreover, is absent from most of the forests inhabited by the other species.

K 1 and K 2. In our area *Cichladusa arquata* is more local and is confined to the neighbourhood of palms; *C. guttata* is not.

(2) Between members of different genera:

A 2 and D. The *Oenanthe* lives on bare stony ground, the *Turdus* on ground with vegetation.

A 2 and L 2. Both forage over the same ground but the *Turdus* is much bigger than the *Erythropygia*.

B and C. No grounds for excluding ecological overlap. In the zone where they both occur the *Neocossyphus* is much rarer than the *Geokichla* and much rarer than it is in the Lowland zone, where the *Alethe fülleborni* is absent.

B and H. The *Geokichla* is much larger than the *Sheppardia*.

B and J 1. Ecological overlap probable. *Alethe fülleborni* and the *Geokichla* are much the same size and they feed in the same stratum, on various invertebrates and a few berries.

B and J 2. The *Geokichla* is much the bigger bird.

B and M. As preceding.

C and G 2. Ecological overlap possible; but the *Neocossyphus* probably feeds more on ants than the *Cossypha*.

C and H. *Neocossyphus* is much bigger than *Sheppardia* (and very rare in their common zone).

C and J 1. Ecological overlap is not excluded but the *Neocossyphus* is altogether rarer than the *Alethe*.

C and M. *Pogonocichla* is much the smaller bird.

D and L 2. *Oenanthe* lives on bare stony ground, *Erythropygia* on bushy ground.

F and G 3. The stonechat tends to live in more woody herbage in drier and more open spaces.

F and G 3. The *Erythropygia*, which is much the rarer, inhabits taller evergreen bush than the *Cossypha*, which is content, for example, with shrubby growth in gardens.

G 2 and M. Ecological overlap not excluded but

neither is numerous where they both occur and the *Pogonocichla* is very rare.

H and J1. The *Sheppardia* is one-third the size of the *Alethe*.

H and J2. Ecological overlap not excluded, but *A. montana* seems very local and has not actually been obtained in the same forest patch as the other bird.

H and M. As preceding.

J2 and M. As preceding.

K1 and L1. *Cichladusa arquata* is associated with palms and houses; *Erythropygia leucophrys* is not.

K2 and L1. *Cichladusa guttata* feeds more on ground with low dense overhead cover than the *Erythropygia* does.

SYLVIIDAE

A *Acrocephalus baeticatus*: 1*f*.
B *Seicercus ruficapilla minulla*: 2*a*(2), 3*a*(2).
C *Bradypterus brachypterus moreaui*: 1*f*, 2*d*.
D1 *Sathrocercus c. cinnamomeus*: 3*a*(4), 3*b* (bush outside the edge of Highland Forest).
D2 *S. mariae usambarae*: 2*a*(3), 3*a*(3).
E *Calamoecetor l. leptorhyncha*: 1*f*, 2*d*.
F *Calamonastes s. simplex*: 1*d*(2).
G1 *Apalis m. murina*: 3*a*(4).
G2 *A. melanocephala*. *A. m. melanocephala*: 1*a*(2), 2*a*(2). *A. m. moschi*: 3*a*(2).
G3 *A. moreaui moreaui*: 2*a*(3).
G4 *A. flavida golzi*: 1*d*(1).
G5 *A. caniceps tenerrima*: 1*a*(1), but only on the coast, not in the rich foothill forests.
G6 *A. rufifrons rufidorsalis*: 1*d*(2).
H *Artisornis metopias*: 2*a*(4), 3*a*(4).
J1 *Sylvietta w. whytii*: 1*c*(3).
J2 *S. brachyura leucopsis*: 1*d*(1).
K1 *Eremomela scotops occipitalis*: 1*c*(2).
K2 *E. griseoflava abdominalis*: 1*d*(1).
L *Camaroptera brevicaudata erlangeri*: 1*a*(4), 2*a*(4). (Rich thick growth such as occurs round the outside of Evergreen Forest and occasionally elsewhere.)
M1 *Cisticola cheniana heterophrys*: 1*c*(1), 1*e*(3).
M2 *C. emini teitensis*: 1*d* (only on occasional rocky slopes).
M3 *C. erythrops sylvia*: 2*c*(1), 2*c*(2).
M4 *C. galactotes haematocephala*: 1*c*(1), 1*e*(3).
M5 *C. natalensis littoralis*: 1*c*(1).
M6 *C. brachyptera reichenowi*: 1*c*(1), 2*b*.
N *Heliolais erythroptera rhodoptera*: 1*e*(3).
O *Melocichla mentalis orientalis*: 1*e*(3), 2*b*.
P *Prinia subflava tenella*: 1*e*(3), 2*c*(1), 2*c*(2).

Analysis of cases of habitat overlap

(1) Within genera:

M1 and M4. On the coast these birds often occur together in a combination of grass and low shrub, and ecological overlap is most probable. Yet elsewhere the two species have distinct ecological preferences, *Cisticola cheniana* for harsh, rather thorny vegetation, *C. galactotes* for soft, rather marshy vegetation. As Lynes (1930) has remarked, in this area the two species show ecological convergence and both occupy ground that is fully typical for neither.

M1 and M6. *C. brachyptera* is a much smaller bird than *C. cheniana* and it is confined to areas that have isolated trees to serve as song-posts.

M4 and M5. *C. galactotes* is rather smaller than *C. natalensis* but ecological overlap is possible.

M4 and M6, M5 and M6. As for M1 and M6.

(2) Between members of different genera:

A and C. The *Acrocephalus* is mainly a bird of reeds (*Phragmites*), the *Bradypterus* of rushes (*Typha*).

A and E. Apparent ecological overlap.

C and E. Apparent ecological overlap.

B and G2. Possible ecological overlap; the *Seicercus* nests on the ground but forages in the same stratum as *Apalis melanocephala*, which nests 40 ft. or so up.

D1 and G1. The *Sathrocercus* is the bigger bird and it lives in the scrub on the outer edge of the forest; *Apalis murina* is on the trees and works inwards from the forest edge.

D2 and G3. The *Sathrocercus* is much the bigger bird.

F and G6. The *Calamonastes* is the bigger.

G1 and H. *Apalis murina* is arboreal; *Artisornis* is not.

G4 and J2, G4 and K2, J2 and K2. Ecological overlap not excluded; but the *Sylvietta* has a longer beak than the others.

H and L. The *Artisornis* lives on the inner side of the forest edge, the *Camaroptera* outside.

M1 and N. *Heliolais* is so much rarer, more local and more skulking than *Cisticola cheniana* that ecological overlap is probably negligible.

M1 and O. The *Melocichla* is much bigger than the *Cisticola*.

M1 and P. Ecological overlap not excluded but the *Prinia* is not common where *Cisticola cheniana* occurs.

M3 and P. *C. erythrops* and *Prinia* constantly occur within earshot of one another in forest clearings but on the whole the former prefers softer and more bushy vegetation.

N and O, O and P. *Melocichla* is much bigger than the others.

N and P. Ecological overlap not excluded but both present in 1*e*(3) in only small numbers.

PRIONOPIDAE AND LANIIDAE

For the present purpose these two families are combined. The taxonomic distinction between them is the scutellation of the tarsi and biologically they are

not satisfactorily distinguished. If the peculiar gregariousness, affecting also the nesting habits of the genera *Prionops*, *Sigmodus* and *Eurocephalus*, extended to *Nilaus* there would be more grounds for separating the two families, though still not for the present purpose.

A *Prionops poliocephala*: 1*d*(1).
B1 *Sigmodus retzii graculinus*: 1*c*(2).
B2 *S. scopifrons kirkii*: 1*a*(1).
C *Eurocephalus rüppellii*: 1*d*(1).
D *Nilaus m. minor*: 1*d*(1).
E1 *Lanius collaris humeralis*: 2*c*(1), 2*c*(2), 3*c* (wherever there are clear ground and perches from which it can be scrutinized).
E2 *L. cabanisi*: 1*d*(1).
F1 *Laniarius f. funebris*: 1*d*(2).
F2 *L. fülleborni*: 3*a*(3).
F3 *L. ferrugineus sublacteus*: 1*c*(3), 1*e*(2), 2*a*(4), 2*c*(1), 2*c*(2), 3*a*(4).
G1 *Dryoscopus cubla hamatus*: 1*a*(4), 1*c*(4), 1*e*(1).
G2 *D. pringlii*: 1*d*(1).
H1 *Tchagra australis minor*: 2*c*(1).
H2 *T. s. senegala*: 1*c*(3), 1*e*(2).
J *Antichromus minutus anchietae*: 2*c*(1).
K1 *Chlorophoneus n. nigrifrons* (*C. münzneri* and *C. nigrescens* regarded as mere colour-phases): 2*a* (1), 3*a*(1).
K2 *C. sulphureopectus similis*: 1*c*(2).
L *Telephorus quadricolor intercedens*: 1*a*(4).
M *Malaconotus poliocephalus hypopyrrhus*: 1*e*(1).
N *Rhodophoneus cathemagmenus*: 1*d*(2).
O *Nicator chloris gularis*: 1*a*(3), 2*a*(3).

Analysis of cases of habitat overlap

(1) Within genera: no cases of ecological overlap.

(2) Between members of different genera:

A and C. *Eurocephalus* gets much of its food by dropping to the ground; *Prionops* is strictly arboreal.

A and D. *Prionops* is always on the move in flocks; *Nilaus* rare, solitary and stationary. Ecological overlap not excluded, but probably negligible.

A and E2. *Prionops* lives and feeds in thorn-trees, the bigger *Lanius cabanisi* gets its prey mostly by dropping to the ground.

A and G2. As A and D.

B1 and K2. As A and D.

C and D. *Eurocephalus* bigger and largely a ground feeder; *Nilaus* arboreal.

C and E2. Competition not excluded but judged to be negligible. *Lanius cabanisi* localized (in very small numbers) to bare edges of the riverine strip.

C and G2. As A and D.

D and E2. The *Lanius* is bigger, more localized (see above), and largely a ground feeder.

D and G2. Ecological overlap probable but both species are present in such small numbers that it can hardly be effective.

E1 and H1. *Lanius collaris* invigilates bare ground or short turf, *Tchagra australis* lives in bushes.

E1 and J. *Antichromus* is confined to marshy vegetation.

E2 and G2. *Dryoscopus pringlii* is arboreal; for *Lanius cabanisi* see under C and E2.

F1 and N. *Laniarius funebris* is confined to thick scrub in broken ground, *Rhodophoneus* is more widely distributed in ordinary thorny bushes.

F3 and H1. The *Laniarius* is bigger and requires larger masses of thicker bushy growth.

F3 and H2. As F3 and H1.

F3 and J. *Antichromus* is smaller and requires more marshy vegetation than the *Laniarius*.

G1 and L. The *Dryoscopus* lives in the treetops, *Telephorus* in the ground stratum of the forest edge.

G1 and M. *Malaconotus* is much the bigger.

H1 and J. *Tchagra australis* does not require the marshy vegetation of *Antichromus*.

NECTARINIIDAE

A1 *Nectarinia famosa aenigularis*: 2*c*(2), 3*b*, 3*c* (herbage).
A2 *N. nectarinioides*: 1*d*(3).
B *Drepanorhynchus reichenowi*: 3*b*, 3*c*.
C1 *Cinnyris bifasciatus microrhynchus*: 1*c*(2), 1*e*(1).
C2 *C. venustus falkensteini*: 2*c*(2), 3*c*.
C3 *C. mediocris usambaricus*: 3*a*(4).
D1 *Chalcomitra amethystina kirkii*: 1*e*(1), 2*c*(1).
D2 *C. senegalensis aequatorialis*: 1*c*(2).
D3 *C. hunteri*: 1*d*(1).
D4 *C. veroxii fischeri*: 1*c*(2).
E *Cyanomitra olivacea changamwensis*: 1*a*(2), 2*a*(2), 3*a*(2).
F1 *Anthreptes collaris elachior*: 1*e*(1), 1*a*(4), 2*a*(4), 2*c*(1).
F2 *A. tephrolaema rubritorques*: 2*a*(4).
F3 *A. pallidigaster*: 1*a*(1).
F4 *A. neglectus*: 1*a*(2), 2*a*(2).
F5 *A. o. orientalis*: 1*d*(1).
F6 *A. reichenowi yokanae*: 1*a*(4).

Analysis of cases of habitat overlap

(1) Within genera:

D2 and D4. *Chalcomitra veroxii* is localized within the range of *C. senegalensis*, near the coast and preferring more evergreen bush.

F1 and F6. Ecological overlap by no means excluded.

(2) Between species of different genera:

A1 and B. Apparently a case of full ecological overlap, with favourite food-plants (e.g. *Leonotis*) in common.

A1 and C2. The *Nectarinia* is the bigger bird and it has a much longer beak. To some extent the same flowers are, however, visited.

B and C2. As preceding.

C 1 and D 1. The *Chalcomitra* is the bigger bird.

C 1 and D 2. As preceding.

C 1 and D 4. As preceding.

C 1 and F 1. The *Anthreptes* has a shorter beak and frequents more evergreen vegetation.

D 1 and F 1. The *Chalcomitra* is bigger and longer-beaked.

D 3 and F 5. *Anthreptes orientalis* has a shorter beak than the *Chalcomitra*.

E and F 4. *Cyanomitra* feeds at a lower level in the forest than *Anthreptes neglectus* and also has a longer beak.

Ploceidae

For the present purpose only the two biggest subfamilies, the Ploceinae and the Estrildinae, are dealt with. They are considered separately, because nearly all the former are much bigger and heavier birds than nearly all the latter; and if they were considered together an unreasonable number of cases of habitat overlap would be generated, only to be resolved at once on the size-criterion.

Classification within the Ploceinae presents difficulties. About half the members of the subfamily have in the past frequently been united in the genus *Ploceus*, with various subgenera. These have by some authors been elevated to genera. Since I am not satisfied with the various divisions (of whatever rank) that have been proposed of the genus *Ploceus* (*sensu lato*), I prefer not to use them at all.

Ploceidae–Ploceinae

A 1 *Ploceus bicolor kersteni*: 1 *a*(2), 2 *a*(2).
A 2 *P. nicolli*: 2 *a*(1), 3 *a*(1).
A 3 *P. r. reichenowi*: 2 *c*(1), 2 *c*(2), 3 *c*.
A 4 *P. jacksoni*: 1 *d*(3).
A 5 *P. i. intermedius*: 1 *d*(1).
A 6 *P. n. nigriceps*: 1 *d*(3), 1 *e*(1).
A 7 *P. r. rubiginosus*: 1 *d*(3), 1 *e*(1).
A 8 *P. brachypterus suahelicus*: 1 *e*(2), 2 *c*(1).
A 9 *P. aureoflavus*: 1 *d*(3), 1 *e*(1).
A 10 *P. castaneiceps*: 1 *d*(3).
B *Amblyospiza albifrons unicolor*: 1 *e*, 2 *c*(1), 2 *c*(2). Builds mainly in swamps but feeds elsewhere, in part on trees and bushes.
C *Anaplectes melanotis*: 1 *c*(2).
D 1 *Quelea erythrops*: 1 *d*(3), 1 *e*(3).
D 2 *Q. aethiopica*: 1 *d*(3), 1 *e*(3).
E 1 *Euplectes hordeacea changamwensis*: mainly 1 *e*(3), but to a smaller extent also 1 *d*(3).
E 2 *E. nigroventris*: as E 1, but preferences reversed.
E 3 *E. diademata*: 1 *d*(3).
E 4 *E. capensis xanthomelas*: 1 *e*(3).
F *Urobrachya axillaris zanzibarica*: 1 *d*(3).
G 1 *Coliuspasser albonotatus eques*: 1 *d*(3).
G 2 *C. ardens teitensis*: 1 *e*(3).

Analysis of cases of habitat overlap

(1) Within genera:

A 3 and A 8. *Ploceus reichenowi* is arboreal, *P. brachypterus* is not.

A 4 and A 6, A 7, A 9, A 10; A 6 and A 7, A 9, A 10; A 7 and A 9, A 10; A 9 and A 10; D 1 and D 2; E 1 and E 4. All appear to be cases of ecological overlap. A 9 and A 10 are especially alike in all ways.

E 1 and E 2. The first is much the bigger bird and in Usambara (Moreau & Moreau, 1938) it occurs especially in ordinary cultivation, where its favourite food is the coarse-seeded grass *Rotboellia*, and where *Euplectes nigroventris* is uncommon; while the latter is commoner in the riverine strip, where it feeds on the smaller-seeded *Echinochloa* and *Euplectes hordeacea* are few. But this ecological separation by no means holds good elsewhere. Fuggles-Couchman (1943) has described how in another locality the two species hold a mosaic of mutually exclusive territories and the staple food of both is another grass, *Panicum maximum*.

E 1 and E 3. *Euplectes diademata* is much smaller and is rare.

E 2 and E 3. Apparently also a case of ecological overlap, but *E. diademata* is rare.

E 2 and E 4. *E. nigroventris* is smaller than *E. capensis*.

(2) Between members of different genera:

A 3 and B. *Ploceus reichenowi* is more arboreal in feeding than *Amblyospiza*.

A 4 and D 1, D 2; A 6 and D 1, D 2; A 9 and D 1, D 2; A 10 and D 1, D 2; D 1 and E 3, F, G 1; D 2 and E 1, E 2, E 3, F, G 1. As the dry season advances the Queleas get more and more of their food by foraging away from the riverine strip; the other birds do not.

A 8 and B. The *Amblyospiza* has a much stronger beak.

E 3 and F, E 3 and G 1. The *Euplectes* is a much smaller bird than the others (and is rare).

A 4 and E 1, E 2, E 3, F, G 1; A 6 and E 1, E 2, E 3, E 4, F, G 1, G 2; A 9 and E 1, E 2, E 3, E 4, F, G 1, G 2; A 10 and E 1, E 2, E 3, F, G 1; D 1 and E 1, E 2, E 4, G 2; D 2 and E 1, E 2, E 4, G 2; E 1 and F, G 1, G 2; E 2 and F, G 1, G 2; E 4 and G 2; F and G 1. All appear to be cases of ecological overlap. E 3 is, however, a rarity.

Ploceidae–Estrildinae

A 1 *Spermestes cucullatus scutatus*: 1 *c*(1), 1 *e*(3).
A 2 *S. n. nigriceps*: 2 *c*(1).
B *Amauresthes fringilloides*: 2 *c*(1).
C *Odontospiza caniceps*: 1 *d*(2).
D *Spermophaga ruficapilla cana*: 1 *a*(3), 2 *a*(3).
E *Cryptospiza reichenowi australis*: 2 *a*(3), 3 *a*(3).
F *Amadina fasciata alexanderi*: 1 *d*(2).
G *Hypargos niveoguttatus*: 1 *a*(4).

H *Mandingoa nitidula chubbi*: 1*a*(4), 2*a*(4).
J *Pytelia m. melba*: 1*d*—rare on edges of riverine strip.
K1 *Lagonosticta senegala somaliensis*: 1*d*—especially round houses.
K2 *L. rubricata* subsp.: 1*e*(4)—especially round houses.
L *Coccopygia melanotis kilimensis*: 2*c*(1), 2*c*(2), 3*c*.
M1 *Estrilda astrild minor*: 2*c*(1), 2*c*(2), 3*c*.
M2 *E. rhodopygia centralis*: 1*d*(2).
M3 *E. subflava clarkei*: 1*d*(3).
N1 *Uraeginthus bengalus ugogoensis*: 1*e*(4).
N2 *U. cyanocephalus*: 1*d*(2).
O *Hypochera ultramarina* subsp.: 1*d*—especially round houses.
P *Vidua macroura*: 1*c*(1), 1*e*(3).
Q *V. fischeri*: 1*d*(2).

Analysis of cases of habitat overlap

(1) Within genera: none.

(2) Between members of different genera:

A2 and B. The latter is the bigger bird.

B and L, B and M1. *Amauresthes* is much bigger than the other.

D and E. The first has a far heavier beak and depends largely on hard-seeded *Olyra* grass.

G and H. The first is the bigger bird.

A1 and P; A2 and L, M1; C and F, M2, N2, Q; F and M2, N2, Q; K1 and O; K2 and N1; L and M1, N2, Q; N2 and Q. All apparent cases of ecological overlap.

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THE ECOLOGY OF SOME INFUSORIAN COMMUNITIES OF INTERTIDAL POOLS

By E. FAURÉ-FREMIET, *Collège de France, Paris*

(With Plate 2)

1. INTRODUCTION

The intertidal pools on the Concarneau shore, those at least which are consecutively covered and uncovered by every tide, offer a nearly constant infusorian fauna, comprising a fair number of individuals, but a limited number of species. This limitation of the fauna seems to depend on the characteristics of the habitat, and particularly on the rapid alterations of the physico-chemical properties of the sea water left in the rock-basins by the ebb tide. During this period of isolation, the sea water is concentrated by evaporation, heated by the sun, alkalized, and grows richer in oxygen owing to the photosynthetic activity of the algal flora.

Legendre (1909, 1922, 1923, 1930) noticed that the temperature of the water in these pools can rise from 18 to 27° C.; its density from 1021 to 1031; its amount of oxygen from 0 to 16·7 mg./l.; and its pH from 8·25 to 9·1. Consequently the infusorian fauna in the pools can only include those species which are eurythermal, euryhyaline and euryionic.

Another fact must be pointed out: the infusorian fauna in the pools, if examined at low tide when the habitat is isolated, seems to be nearly constant; but every tide overflows the pools and the water in them is more or less stirred and renewed while the restricted character of the environment disappears. The question is then to know how a definite infusorian community can remain within the limits of an environment whose liquid content is mixed twice a day with the open sea water. It must be pointed out that there are no interdependent relations between the various prominent species composing the infusorian community, whereas such relation does exist between some of them and the algal flora spreading over the bottom of the intertidal basins. Before dealing with the question we propose to answer, it is important to know the way of life of the infusorian species which remain apparently or actually stationary in the intertidal pools.

2. SPECIES EXAMINED

The species are unequally distributed among all the Ciliate orders. The more common species found were:

Holotricha Gymnostomata
- *Prorodon discolor* Ehrb. var. *marinus* A. Kahl
- *Trachelocerca phoenicopterus* Cohn
- *T. fusca* A. Kahl
- *Coleps tesselatus* A. Kahl

Holotricha Hymenostomata
- *Frontonia* sp.
- *Porpostoma notatum* Mobius

Oligotricha
- *Strombidium sulcatum* Clap. and Lach.
- *S.* (*Strobilidium*) *oculatum* Gruber

Heterotricha
- *Condylostoma patens* Stein.
- *C. patulum* Clap. and Lach.

Hypotricha
- *Diophrys scutum* Duj.
- *Uronychia transfuga* O. F. Müller
- *Holosticha* sp.

Peritricha
- *Vaginicola crystallina* G. Entz Sen.
- *Zoothamnium duplicatum* A. Kahl

The ciliates are not limited to the 15 species which have just been mentioned. The occurrence of a few other species has been observed; but being small in number and in size they have not been listed. Moreover, their populations grow only under artificial conditions, i.e. after their isolation and stagnation *in vitro*.

3. ECOLOGICAL CHARACTERISTICS OF THE SPECIES EXAMINED

We will not dwell on the members of the family Vorticellidae, since the question we want to deal with does not apply to Infusoria anchored on a fixed support (Algae, etc.). Moreover, *Vaginicola crystallina* and *Zoothamnium duplicatum* are not exclusively localized in the pools; they are much more widely distributed on the littoral.

On the other hand, all the other Infusoria belong to free-swimming and active species. From the point of view of ecology, they can be divided into three different types:

(*a*) The histiophagic predators feeding occasionally or necessarily on animal tissues; their occurrence is connected with that of small Metazoa, Copepoda, Amphipoda, Cirripedia, Mollusca, Annelida, etc., which constitute their food when injured or decayed.

Among this type, *Porpostoma notatum* is commonly found swimming in the pools hunting for food, without ever constituting numerous populations. They swim swiftly and steadily covering thus a fair distance, so that they are widely spread all over the littoral.

On the other hand, *Coleps tesselatus* and *Prorodon discolor* are more frequently to be found only in

contact with the thin and muddy coat of organic detritus covering the bottom of the basins, between small pebbles and algal vegetations.

After a rapid and abundant feeding, *P. discolor* remains motionless for a long while inside an adhesive cyst; when it is starving, it does not swim as rapidly and does not cover as much distance as *Porpostoma*.

Coleps tesselatus is a sluggish Infusorian coated with a calcareous integument which plays in this habitat the part of a scavenger, similar to that of *C. hirtus* in fresh water.

(*b*) The thigmotactic Infusoria are represented in the pools by various types.

Let us mention first a predator of large size, *Trachelocerca phoenicopterus*. The individuals are not easy to observe because they glide swiftly on solid surfaces, worming themselves into detritus and gravel among which they seem to disappear, adhering to them if disturbed. This species can also be found scattered in the sand all along the shore. *T. fusca* is distributed the same way, but more abundantly.

Phytophagous species such as *Condylostoma patulum*, chiefly a diatom-feeder, multiply often with a comparative abundance at the bottom of the pools; the allied species *C. patens* whose only morphological difference from the former is a thinner and more contractible body, feeds also on spores, on brown flagellates and occasionally on smaller Infusoria such as *Strombidium sulcatum*. Like the latter it can be free-swimming, but both of them occur chiefly in the pools situated at a higher level than that of the high neap tide.

Chlamydodon triqueter seems to feed on blue-green Algae (like *C. mnemosyne* in brackish water). This peculiar Infusorian is characterized by a kind of ventral sucker. The scattered individuals are scarce and multiply very slowly; they present but uncertain ecological characteristics.

Among Hypotricha, an undetermined *Holosticha* of large size appears in small numbers under the same conditions as *Trachelocerca phoenicopterus*; like this very large Gymnostoma it may be found outside the pools in the sands along the beaches. This *Holosticha* resembles many thigmotactic Infusoria in being very unstable, and can burst when in contact with the air-water interface.

Two widely distributed species, *Diophrys scutum* and *Uronychia transfuga*, are represented in the pools by a rather large number of individuals which seem to feed on various sorts of food.

Consequently, it appears that, except perhaps in the imperfectly known case of *Chlamydodon triqueter*, none of the species above mentioned can be considered as a specific inhabitant of the pools; the thigmotactic Infusoria can to a certain extent maintain themselves on the surfaces which remain immovable while the water is renewed. But the probable dispersion of a great number of individuals with every tide seems to correspond to the extremely large distribution of these species and to the fact that their populations never reach a very great number in this periodically renewed environment.

The last group of Infusoria examined shows a different case.

(*c*) The free-swimming Infusoria of the planktonic kind are represented by two Oligotricha species, *Strombidium sulcatum* and *S. oculatum*. The first is essentially ubiquitous and multiplies particularly in the pools situated at a high level, or after artificial stagnation *in vitro* of the water normally renewed by every tide. The second species, on the contrary, is one of the most typical inhabitants of the habitat we are studying.

In the pools *S. oculatum* (Gruber, 1884) reaches a high population density, between 200 and 250 individuals per ml., which is far above that reached by all the other ciliate species. They show a very marked positive phototaxis and gather chiefly in the superficial layer of the water. They swim rapidly, at the speed of three to four millimetres to the second, which gives them a high 'diffusion coefficient', though less high than that of *Porpostoma*.

Such an individual mobility together with such a density of population is at first difficult to understand in a liquid environment renewed with every tide; particularly if we recall that *S. oculatum* is neither to be found in the water nor among the Algae on the whole littoral outside the pools, nor in the plankton collected near the shore. As a matter of fact this species seems to be strictly limited to the discontinuous habitat formed by the pools, and must be the special object of the question proposed at the beginning of this paper.

4. THE CASE OF *STROMBIDIUM OCULATUM*

The shape of this Infusorian is regularly conical or ovoid; its length is about 60–80μ. Dark green coloured, it shows at the anterior end a red pigment spot or a spreading accumulation of the same pigment under the membranellae of the dorsal fringe. The green colour is due to some unicellular Algae, probably symbiotic, filling the cytoplasm. They are not Chlorellae, and as in *Strombidium mirabile* (Penard, 1916) of fresh water, they are more likely to be *Chlamydomonas* with a red stigma; they are generally in the state of spores, but are occasionally able to become biflagellate, piriform, moving individuals.

Again, as in the case of *Strombidium mirabile*, a certain number of these spores decay and are probably digested but for their stigma, whose red corpuscles and starch granules are brought together at the apical end of the Infusorian, constituting the limited

Rocky basin, close to the laboratory, used for continuous observation of the rhythm of *Strombidium oculatum*

or widely spread 'ocular spot' first described by Gruber. On the other hand the pyrenoids of the decayed Algae are to be found scattered in the cytoplasm of the host together with some pieces of chloroplasts, among the unaltered spores.

The whole posterior end of the body, below the girdle of radial trichocysts reaching through the ventral face as far as the antapical end, is covered as in *S. testaceum* (Anigstein, 1913) and *S. mirabile* (Penard, 1916) with a refringent, resistant and thin pellicle; this pellicle is generally lifted by fixatives; it is composed of lamellae of an irregular polygonal shape of a carbohydrate composition apt to be turned into violet by iodine.

S. oculatum is partly diatom-feeding; it shows very active multiplication by means of the kind of lateral budding generally characteristic of the fission process of the Oligotricha.

The positive phototaxis of this Infusorian makes it very easy to study. If a few litres of water from the pool are poured into a cylindrical vessel wrapped in a sheet of black paper out of which a small window has been cut, and the vessel is placed in a dark room, with the window lighted by a beam coming from an electric bulb with a condenser, *Strombidium* gather rapidly into the bright zone and flock as a dark green cloud in contact with the glass, where they are easily collected with a fine pipette. In about 15–20 min. time, nearly the whole of the *Strombidium* population contained in 5 l. of water can be thus isolated so that a quantitative study and various experiments are easily made.

A thorough study of a particular pool shows that *S. oculatum* are either very scarce or absent when the habitat has just been isolated by the ebb tide; but these Infusoria reappear soon afterwards and their number increases so rapidly during the next hour that their density of population soon becomes the same as before in the superficial layers of water, whether the sky is overcast or bright.

Throughout low tide, *Strombidium* remain very active and many individuals divide; but 15–20 min. before the flowing tide reaches the pools, whatever the time of the day tide may be, it can be observed that the individuals decrease quickly in number and then disappear almost entirely when the pool starts being in contact with the ocean.

When examining what happens in a vessel containing some water removed from the same pool at any time during the low tide, we observe that 15–20 min. before the external water reaches the pool, the phototaxis of *S. oculatum* isolated *in vitro* decreases rapidly and then becomes negative. The Infusoria can be seen gathering into a thick cloud opposite to the light and some of them, slowly revolving, start to encyst themselves when in contact with a solid surface; others soon become equally still when close to those already encysted, and wide adhesive green spots are the only traces which remain of the thousands of free-swimming Infusoria observed during the low tide.

The experiments made *in vitro* and *in situ* show that the excystment occurs spontaneously, apart from any direct influence of the tide, not during the next low tide, but at the beginning of the following one. *S. oculatum* offers thus another example of 'tidal rhythm' similar to that of *Convoluta roscoffensis* or *Euglena limosa* (cf. Bohn, 1903*a*, 1904*b*, Bohn & Drzewina, 1928; Bracher, 1919, 1929, 1937; Gamble & Keeble, 1903*a*, *b*; Gard, 1919, 1922). Owing to this phenomenon, this essentially mobile Infusorian is able to keep within the limits of the pools even during the high tide.

This rhythm results in a recurrent physiological cycle taking nearly a whole day, so that the Infusoria lead a free active life for a period of about 6 hr., during which they keep dividing, then encyst themselves and remain in a resting state for a little longer than 18 hr.

As happens with *Convoluta roscoffensis* and *Euglena limosa*, the 'tidal rhythm' of *Strombidium* gradually loses its regularity and disappears when the Infusoria are kept *in vitro* away from their genuine environment, whereas *in situ* it remains exactly connected with the rhythm of ebb and flow. This question has been examined elsewhere (Fauré-Fremiet, 1948) with the details of experimental results. Let us only point out that the exactness of the physiological rhythm is actually nothing but a statistical effect resulting from the observation of a great number of individuals, and that in the normal habitat, every high tide practises a sort of selection, carrying away and eliminating the *Strombidium* excysted too early or encysted too late. Thus individuals having a rhythm of activity not co-ordinated with the tides are automatically eliminated from the habitat.

5. SUMMARY

1. The Infusorian fauna of the intertidal pools of the Concarneau shore includes about 14 free-swimming species.

2. The study made during low tide of the isolated habitat shows that the composition of this community as well as the relative importance of its component species remain nearly constant, in spite of the fact that most of the water is renewed by every high tide.

3. The apparent stability of the community is maintained in two different ways:

(*a*) In most of the observed cases, this stability is probably the result of a kind of balance between the distribution inside and outside the habitat of individuals belonging to eurythermal, euryhyaline and widely spread species.

(*b*) With *Strombidium oculatum*, this stability is the

result of a physiological rhythm preserving the free-swimming individuals from the dispersive action of the tide by enclosing them in a cyst adhering to solid surfaces. We have then to deal with a case of adaptation to the intertidal conditions of life by means of a 'tidal rhythm' similar to that of some other organisms living on the littoral, though in very different habitats topes, such as *Convoluta* and *Euglena limosa*.

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THE HISTORY OF THE SPECKLED WOOD BUTTERFLY (*PARARGE AEGERIA*) IN SCOTLAND, WITH A DISCUSSION OF THE RECENT CHANGES OF RANGE OF OTHER BRITISH BUTTERFLIES

By J. A. DOWNES, *Zoology Department, University of Glasgow*

(With one Map)

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1. INTRODUCTION

It is well known among naturalists that the range of speckled wood butterfly, *Pararge aegeria* (L.), in the south of England has fluctuated considerably. For most of the nineteenth century it appears to have been generally distributed, but towards the end, and in the first two decades of the twentieth, it disappeared from many places, particularly in the south-east, where it had formerly been common. This contraction of range was discussed in several papers, such as those of Burrows (1916) and Gibbs (1916). More recently, during the past fifteen years or so, it has reappeared in many of its old localities (see, for example, Ford, 1945, p. 140; Jackson, 1944).

This butterfly has also greatly altered its range in the north of England and in Scotland during the last hundred years, but the facts have never been summarized and are not generally known.* It seems useful now to give an account of these changes, since two recent discussions of the distribution of the species (Ford, 1945; Beirne, 1947) have led to conclusions that the full facts do not support. Both these authors describe it as absent in the north of England, and confined in Scotland to western Argyllshire and Inverness-shire, and discuss this range on a geological time-scale. But it will be shown below that it inhabited the north of England and extensive areas in Scotland until very recently, and became restricted to the range that Ford and Beirne describe only during the last hundred years.

The case of the speckled wood leads naturally to a consideration of the recent changes in range of other butterflies, and the last part of the paper contains an account of these changes and a discussion of their implications.

* But see footnote, p. 135.

2. THE ORIGIN OF THE RECORDS

To collect the records given below, I have searched the files of the Entomologist's Monthly Magazine, the Entomologist and the Entomologist's Record from their inception until 1946, and of the Scottish Naturalist (known between 1892 and 1911 as the Annals of Scottish Natural History) until it stopped publication in 1939. Other records are derived from various journals and handbooks. The records of the large tortoiseshell and of the silver-washed fritillary, discussed on p. 136, are not the result of a systematic search, but are merely those encountered during the preparation of other parts of this account.

I should like to thank several correspondents for valuable assistance. Mr John Boyd, Largs, gave me a number of very interesting references to old Scottish records. Dr A. C. Stephen, Edinburgh, supplied other references, and information about the specimens in the Royal Scottish Museum. Several unpublished records are contained in a letter from Mr J. L. Campbell, of Canna; and Mr H. M. Edelsten enabled me to examine the British Museum specimens.

3. THE RANGE OF THE SPECKLED WOOD IN THE NORTH OF ENGLAND

In the northern counties of England the speckled wood was once widespread. There are two specimens in the British Museum collection labelled 'Preston, Elwes collection' and 'Preston, 25/6/87, Elwes collection'. Forsythe (1905) says of it '"Fairly common near Witherslack [Westmorland] some years ago" (G. Loxham). This species is now extinct in this district.' Ford (1945) also notes that it has occurred at Witherslack in the past, and may be referring to the

same record. Porritt (1883) gives its distribution in Yorkshire as 'Bramham, Edlington Wood, Huddersfield (formerly), Ledsham (common), Pontefract, Scarborough, Sheffield, Wakefield, Wentridge and York (1842).' Further north, Robson (1899) says that in Northumberland and Durham it was 'apparently well distributed over both counties half a century or more ago. "Mr R. Currie took it near Belford in the spring of 1826." Wailes. [*Sic*]. It was also in Selby's Twizell List and the specimens were in the collection when it was examined by me. Mr Wm. Backhouse found it at Castle Eden Dene and Mr E. Backhouse, Jun., took it near Sunderland. There are no recent records of its occurrence and I never took it myself.' Finally Bolam (1926), writing of the species in Northumberland, says it was 'not uncommon in Countess Park [near Bellingham] and Garret Hot Woods in August, 1896, and I saw it there again in 1920. Selby recorded it from Twizell where I used to see it up to twenty years ago, as also at Belshill, Chillingham, Middleton Hall (above Wooler), Crawley Dene, Glanton and Eslington, to instance but a few localities.' The last six places are all in the north-eastern part of the county.

It will be noticed that all these authors refer to the species as rarer than formerly, and in some cases as extinct. Bolam's record for Northumberland in 1920 is, in fact, the only one I know for the northern counties of England in the twentieth century. Clearly it is now much rarer than it used to be in this area, and probably it is extinct. Ford (1945) suggests it may still exist in south Yorkshire.

This account of the speckled wood in northern England is not intended to be exhaustive, and other old records could have been included. But enough has been said to show that it used to occupy the area extending southward from the Scottish Border to the northern limit of its present-day range (see map 1 of Ford, 1945).

4. THE RANGE OF THE SPECKLED WOOD IN SCOTLAND

In Scotland, as in England, the speckled wood is characteristic of shady wooded regions. It occurs only at low elevations and is thus mainly confined to the coast, the margins of sea lochs and the lower parts of certain valleys. It will be convenient to discuss its occurrence in the eastern and western halves of the country separately. All its known localities are indicated on Map 1.

Buchanan White (1872) summarizes its status in Scotland as 'local, rare in the north' and says that it occurs in the 'provinces' of Tweed, Forth, Tay, Dee, Solway, Clyde and Argyll. It will be seen below that this is an accurate account of its range during part of the nineteenth century, but that at the present day it is much restricted.

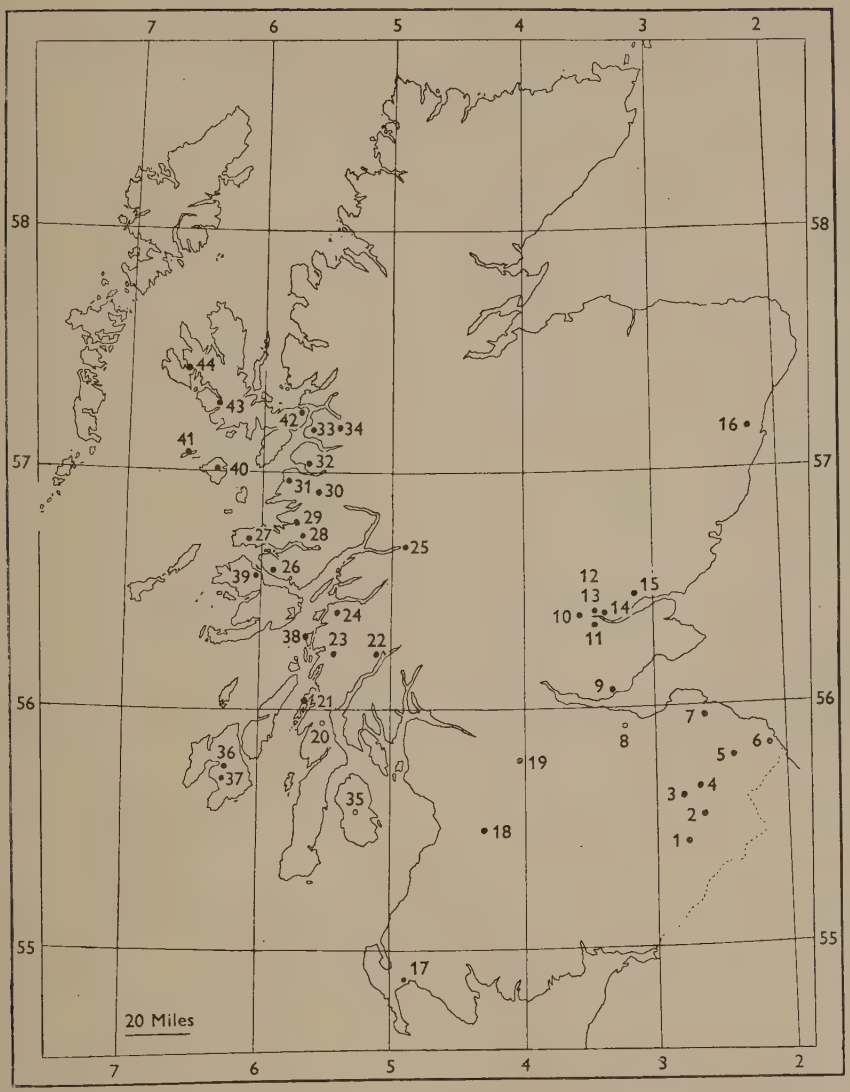
In south-eastern Scotland, Bolam (1926) says 'About Berwick it was [more than twenty years ago] fairly common on the Whitadder [*sic*] banks from Edrington Castle to Abbey St Bathans, at Ayton and up Ale Water, Galashiels, Lauderdale and doubtless many other places. Whether it has diminished in numbers in any of these localities during the last twenty years I cannot say.' The Whiteadder Water and Ayton are in eastern Berwickshire; the lower part of the Ale Water is in Roxburghshire; and Galashiels and Lauderdale both lie on the county boundary of northern Roxburghshire. Renton (1903), in his list of the Lepidoptera of Roxburghshire, records a single specimen near Ormeston Mains, Teviot, on 5 May 1901. Evans (1897) writes that 'thirty to thirty-five years ago I used to meet with this butterfly in a plantation at Biel [near Dunbar, East Lothian] but have not since found it anywhere in the Lothians.' Somewhat earlier than this, however, Lowe & Logan (1852) say that *P. aegeria* was 'not infrequent in woods' in Midlothian during the previous few years.

From north of the Forth, there is an undated specimen in the Royal Scottish Museum, Edinburgh, taken at Aberdour, Fifeshire, by Dr R. H. Traquair. Traquair died in 1912.

There is a considerable group of records from around the Tay estuary. Buchanan White (1870) says '*P. aegeria* is a very local species and never appears to be abundant. It occurs on Kinnoul Hill and near Muirhall [both near Perth] and is double brooded.' The same author, in 1871, repeats these localities and adds Rossie Priory (between Perth and Dundee). Moncreiffe (1878) says that two or three specimens have been taken on Moncreiffe Hill, which is also in the immediate neighbourhood of Perth. It may have persisted in this region for some time, as Wylie (1914 *a* and *b*) records it from a hedgerow near Tibbermore; and in another paper of the same date as 'rare, confined to cliffs, Kinfauns.' These records are undated but refer to some period before 1908 and 1911 respectively, the years in which the papers were actually prepared. (It may be explained that the 'cliffs' at Kinfauns are not bare coastal cliffs, but the rocky loosely wooded slopes of the Sidlaw Hills where they come down to the Carse of Gowrie.)

The only eastern record north of the Tay area appears to be the one in Barrett's handbook (1893), where it is stated that 'Mr W. Reid says that two have been taken at Hazlehead, Aberdeenshire.' Hazlehead is three miles east of Aberdeen, in country that appears to be quite suitable for this butterfly. Reid was a well-known collector of the day and there is no reason to doubt this outlying record. Perhaps Buchanan White (1872) is also referring to these specimens when he records the species from the 'province of Dee'.

In the western half of the country there are records



Map 1. Known distribution of the speckled wood butterfly in Scotland during the past century. Solid circles mark precise localities, open ones those given only approximately. 1, Ormiston Mains; 2, Ale Water; 3, Galashiels; 4, Lauderdale; 5, R. Whiteadder; 6, Ayton; 7, Biel; 8, Midlothian (County of); 9, Aberdour; 10, Tibbermore; 11, Moncreiffe Hill; 12 and 13, Muirhall and Kinnoul Hill; 14, Kinfauns; 15, Rossie Priory; 16, Hazlehead; 17, Luce Bay; 18, Ballochmyle; 19, Cadzow; 20, Knapdale; 21, Tayvallich; 22, Inveraray; 23, near Kilmelfort; 24, Oban; 25, Kinlochleven; 26, near Loch Aline, in Morven; 27, Ardnamurchan; 28, near Strontian, in Sunart; 29, Kinlochmoidart; 30, south side of Loch Morar; 31, Morar; 32, Inverie, in Knoydart; 33 and 34, south of Loch Duich; 35, Arran; 36, Bridgend, Islay; 37, R. Duich, Islay; 38, Seil; 39, between Salen and Tobermory, Mull; 40, Loch Scresort, Rhum; 41, Canna; 42, Kyleakin, Skye; 43, Loch Harport, Skye; 44, Dunvegan, Skye.

of the butterfly from three localities south of the Clyde. Gordon (1913) says 'Mr J. Garraway took it in the shady part of Alticry Glen, Luce Bay' (Wigtownshire: date of capture not stated). Duncan (1872), in his 'Lepidoptera of Ayrshire' says that 'the species is rather local, and nowhere abundant in the county. The only locality known to me is Ballochmyle Bridge [near Mauchline], in an open wood.' Cameron (1876), who had access to lists provided by various collectors, records it as 'Frequent, Cadzow Castle [Lanarkshire, near Hamilton] and Ballochmyle Bridge.' This Ballochmyle record is presumably derived from Duncan, and it appears from Dalglish (1901) that the Cadzow record is attributable to Dr H. Colquhoun.

On the Argyllshire mainland, Walker (1887) took it in July of that year but gives no precise locality. He appears to have been collecting in Knapdale at the time. Barrett (1893) says it has been found in Knapdale, and may be referring to Walker's note. However this may be, A. M. Stewart took it at Tayvallich, a few miles to the north, in August 1900, his record being given both by Dalglish (1901) and Morton (1931). Mr J. L. Campbell found it there again about 1922 (private communication). Dalglish (1901) gives an undated record by Dr T. Chapman at Inveraray, Loch Fyne. Henderson (1943) found it at Kinlochleven in early July of that year.

In western Inverness-shire, Downes (1947) records it as fairly common at Kinlochmoidart on 28 June 1945. Morton (1931) found that it was fairly common at Morar during July 1930, and Campbell (1945) observed it there again on 26 April 1945. Mr Campbell tells me that he has also taken it in numbers at Inverie in Knoydart, and suggests that it probably occurs in suitable woods as far north as Glenelg.

On the inner isles, it extends from Arran in the south to Skye in the north, and thus closely parallels its mainland range. For Arran, Dalglish (1901) gives an undated, and presumably already rather old, record of Colquhoun's. Much later, Morton (1931) records that Mr A. M. Stewart saw the butterfly in Arran in August 1929.

On Islay, four specimens were taken at Bridgend by R. W. Sheppard between 26 April and 5 May 1912 and are now in the British Museum collection. Wilks (1945) records that he found the species along the river Duich (a few miles south of Bridgend) in July and August 1940. Downes (1947) mentions a single specimen found by Dr H. D. Slack on Seil Island (near Oban) on 21 July 1946. In Mull there are several records, none of them giving a precise locality. Morton (1931) mentions a specimen taken there about thirty years previously. There is a specimen in the Royal Scottish Museum, taken by Lt.-Col. Logan Home in July 1921. Finally, Laidlaw (1932) found the butterfly abundant in one locality on the east coast, in July 1930 and July 1931.

Campbell (1946) notes the occurrence of the butterfly as a 'vagrant' in Canna in 1945. Mr Campbell, whose home is on Canna, has informed me that on that occasion two specimens were taken and another seen, and that he has not seen any more since then. As Canna is about three miles from Rhum, and ten miles from the nearest point of Skye, the butterfly seems to be able to cross short distances over water. It has been recorded from Skye, where it reaches its northern limit, by Tutt (1896) and Dale (1890). The latter says 'The shady woods and wet climate of Dun[v]egan in the Isle of Skye seem especially adapted to its requirements.' I cannot trace the original source of the Skye records.

In addition to these west of Scotland records, Ford (1945) indicates a number of localities for the species on his map 1, but does not give any additional information in the text. They are as follows: Argyllshire—Knapdale, near Kilmelfort, Oban, near Lochaline in Morven, in Ardnamurchan, and near Strontian in Sunart; Inverness-shire—south side of Loch Morar, and two localities south of Loch Duich; Inner Isles—Islay, near River Duich; Skye, Kyleakin and near Loch Harport. This set of records confirms very precisely the range already traced for the species in the west of Scotland north of the Clyde. Some of them may be duplicates of records already given.

Clearly, at one time or another since about 1850, the speckled wood has occurred in most of the coastal regions of Scotland from the Borders to Aberdeen on the east side and to Inverness-shire (including Skye) on the west. But since 1913 at the latest (Gordon, 1913—Luce Bay), there are no records except from the western mainland of Argyll and Inverness, and the adjacent islands from Arran to Canna. From this area however, there are at least twelve reports between 1921 and the present day, several of which refer to it as common. The butterfly has thus greatly reduced its range during the last hundred years, and now appears to exist only in this middle western region.

This reduction may have started about 1860–70, for Evans in 1897 records that he had not seen it in the Lothians for over thirty years. Southwards, in Berwickshire and Roxburghshire, it persisted until the early years of this century, but has not been noted there since then. It should, however, be remembered that there is a single record in adjacent Northumberland as late as 1920 (Bolam, 1926). In the Tay area, where it used to occur in several localities, it has not been seen since 1911 at the latest, and had perhaps disappeared rather earlier than this. In the west, it is probably now extinct south of the Clyde: two of these southern records (Cadzow and Ballochmyle) date from the 1870's; but in Galloway it maintained its hold until somewhat later.

In Arran and north of the Clyde to Inverness-shire however, it seems to have decreased little, if at all, over a long period. There are old records from Arran, Islay (1912), Knapdale, Tayvallich, Inveraray, Mull and Skye, while within the last twenty-five years it has been found in Arran, Islay, Seil, Mull, Canna, Tayvallich, Kinlochleven, Moidart, Morar and Knoydart. The group of six records from Seil to Knoydart in the last five years even suggests that it may be on the increase again.

5. DISCUSSION

(*a*) *The recent changes of range of the speckled wood*

The history of this butterfly in Scotland and the north of England is of especial interest because Ford (1945) and, more briefly, Beirne (1947) have both discussed it in their accounts of the origin and history of various British Lepidoptera. Both authors consider only its present-day restricted range and seem to have overlooked its recent history. On this basis, Ford (p. 314) appears to consider that during the last Pleistocene glaciation the species was exterminated by the cold over much of its range, and was generally driven southwards except for a colony that became isolated on the warm west coast of Scotland, and that these two ranges have remained separated ever since. This, on the facts presented above, is clearly an untenable hypothesis. He considers that something similar has happened in the case of two other species also, the brown argus (*Aricia agestis* (Schiff.)) and the chequered skipper (*Carterocephalus palaemon* (Pall.)). In these two cases the hypothesis may well be true, as both have evolved distinct races in the north; but it has not been suggested that the normal Scottish form of *Pararge aegeria* is taxonomically separable from the English one, nor would one expect this in view of its history.

Beirne (1947, pp. 332 and 340), who may have derived his map of the range of the speckled wood from that given by Ford, observes that it tends to have a south-western and western range. He deduces, apparently from this fact alone, that the species arrived in Britain during a warm Pleistocene period and implies that its range was reduced in the last glacial phase of the upper Pleistocene glaciation. Again both the facts and the deduction are hardly in line with the account of the species just given.

To summarize, it appears that the present range of the speckled wood in Britain—the south and midlands of England, Wales, and western Argyll and Inverness and the Inner Isles in Scotland—is not a phenomenon of long standing, to be explained on a geological timescale, but represents an extremely recent (and rather well-documented) contraction of a range that used to cover the whole of England and Wales, and Scotland up to Aberdeenshire, Inverness-shire and Skye. These changes are probably due to delicate alterations in the biological balance or in climatic conditions. The contraction of range has already been reversed in the south of England and there is an indication that the same may be happening in the west of Scotland.*

(*b*) *General considerations on the changes of range of British butterflies*

Analogous and equally well-documented changes in range have been undergone by several other British butterflies in the last hundred and fifty years. The facts are well known to most naturalists interested in Lepidoptera and are summarized by Ford (1945, pp. 138–51). The comma (*Polygonia c-album* (L.)) was once widespread in the south of England. About a century ago it became restricted to the counties of Gloucester, Hereford and Monmouth, but in the last thirty years it has spread again over the south of England, the Midlands and even to the Scottish Border, thus considerably exceeding its earlier range. The white admiral (*Limenitis camilla* (L.)) also became rare and restricted to a few woodland areas in the south and in Suffolk. Since 1920 it has again become widespread and common in the south and south Midlands. The history of the wood white (*Leptidea sinapis* (L.)) has been rather similar. Its former range was probably more extensive than that of the white admiral and included a locality in Cumberland. Early in the present century it became restricted to a few southern woodlands, but in the last twenty years it has extended its range in the south and south Midlands, though not so strikingly as the white admiral. The peacock (*Nymphalis io* (L.)) used to be extremely rare in north England and in Scotland. In the last fifteen years or so it has become widespread and common over much of this area. I have myself found it in large numbers around Glasgow and Loch Lomond, and less commonly in various places in Argyllshire, in 1944–7. It now extends to Caithness and also occurs on several islands, for example, Rhum (Harrison,

* As a result of my earlier note on the speckled wood (Downes, 1947), two short papers on its distribution in the north of England and in Scotland have appeared since the completion of this article (Smith, 1948; Harrison, 1948). Both papers quote several of the above records and give a few interesting additional ones which confirm my general conclusions. Smith found the butterfly in Mull, between Salen and Tobermory, in 1934, and knew of the Kinlochmoidart colony in 1932. Harrison agrees that its range was continuous from the south of England to northern Scotland not so very long ago. He adds a record from Loch Scresort, Rhum, in 1947. For the north of England, he gives old records from the Team Valley (north Durham) and from Keswick (Cumberland), and a recent one (1946) from Castleford, near Leeds. The Castleford record confirms Ford's suggestion that it still occurs in southern Yorkshire.

1945) and Canna (Campbell, 1946). The large tortoiseshell (*N. polychloros* (L.)) was widespread in the south and Midlands until about 1903; it then became extremely local and scarce, but very recently it has begun to spread again. The reduction in range early in the present century may have been much greater than Ford indicates. He says that it was always restricted to the Midlands and southern England, although Beirne (1947) admits that it extended to the north of England. In fact it used to occur rarely but repeatedly in Scotland, extending as far north as Aberdeenshire. The following records were encountered while collecting the data on the speckled wood: one at Melrose, Roxburghshire, 1883 (Beveridge, 1883); one in East Lothian, 1869, and one near Edinburgh, 1861 (Evans, 1897); several in Aberdeenshire, 1872 (Garrow, 1872); 'occasionally' in Aberdeenshire and Kincardineshire (Esson, 1890); four in various localities in Galloway, 1893, 1896 and 1910 (Gordon, 1913) and one in South Knapdale, 1887 (Walker, 1887). It is probably significant that the latest of these records is in 1910. The silver-washed fritillary (*Argynnis paphia* (L.)) which is not mentioned by Ford in his discussion of these changes, is another species that has probably reduced its northern range fairly recently. According to Ford it does not now occur north of Witherslack (Westmorland) and north Yorkshire, while according to Beirne it extends to the north of England. However, as with the large tortoiseshell, I have found several old Scottish records as follows: in some seasons common on Minto Rocks, Roxburghshire (Renton, 1903); at Grant's House and Gordon Moss [Berwickshire] about 1880 (Bolam, 1926); Rossie Priory [Perthshire, near Dundee] and perhaps near Errol (Buchanan White, 1871); one at Luce Bay, Wigtownshire, 1905, (Gordon, 1913); one near Arrochar, Dumbartonshire (Cameron, 1876); in considerable numbers, Lochinver, Sutherlandshire, 1892 (Beveridge, 1892). Again it is probably significant that none of these records are later than 1905. Finally, the black-veined white (*Aporia crataegi* (L.)) used to occur over a wide area in the south of England and Wales. Later it became restricted to a small area in Kent and eventually, about twenty years ago, it became extinct in Britain.

We see, therefore, that there have been major changes in range during the last hundred and fifty years, sometimes an expansion, sometimes a contraction, and sometimes a contraction followed by an expansion, of at least eight of the sixty-eight butterflies usually reckoned as British. If the ten species whose existence in Britain depends entirely on immigration from abroad are discounted, such changes have affected more than 13% of the fauna. In each case the cause of the change is unknown, but there is no adequate reason for assuming that it has been brought about mainly by human agency. (It will be noticed that the restriction and extinction of the large copper (*Lycaena dispar* (Haw.)) has been omitted from the discussion, because this is supposed to have been due to the drainage of the Fens coupled with over-collecting). A decrease of range of woodland species might well be put down to the work of man, but, although such cases have occurred, it is remarkable that three very characteristic woodland butterflies, the white admiral, the wood white, and the speckled wood, have extended parts of their range during the twentieth century. The comma, the peacock, and the large tortoiseshell are all butterflies of open country, gardens and the margins of woods, and feed as larvae on nettle and hops, nettle, and elm respectively. It seems rather unlikely that these habitats have been altered by man both unfavourably and favourably since about 1850 sufficiently to account for the changes in these species. The increase of the peacock and the decrease of the speckled wood (a grass feeder) and of the silver-washed fritillary have occurred largely in the agricultural regions and the fringes of the Highlands of Scotland, where human activity has been relatively constant.

It is also interesting to observe that two of these butterflies, the speckled wood and the wood white, can by no means be reckoned as strong fliers.

The general explanation of these changes is possibly related to the geographical position of Britain, which lies at the northern limit of the range of many butterflies. A species near the limit of its range is probably not sufficiently well established to enable it to survive the more intense occasional or periodic fluctuations in environmental conditions, and so might readily become extinct in certain areas. When more average conditions return, these areas would again become habitable.

As so many great changes have taken place in one hundred and fifty years, it seems very likely that major alterations in the ranges of a large number of British butterflies have occurred within a period of the order, say, of one or two thousand years and have not required the much longer periods of time marked by the onset and retreat of glaciations. If this is so, it is impossible to analyse the present distribution of such animals in Britain in terms of the ordinary concepts of zoogeography with much hope of arriving at a valid conclusion. Certain qualifications must of course be made to this statement, chiefly with respect to species that have formed one or more independent subspecies. The existence of these subspecies clearly indicates that their various ranges, originally different, have never been so greatly altered as to overlap and coincide. But even so there may have been quite considerable changes, for if the ranges of two subspecies expand and eventually meet there is often a process of selection that tends to keep them distinct. This

process is probably acting on the brown argus (*Aricia agestis agestis* (Schiff.) and subspecies *artaxerxes* (F.)) in the north of England, and on the dark green fritillary (*Argynnis aglaia aglaia* (L.) and subspecies *scotica* Watkins) in the Isle of Rhum, at the present day (Ford, 1945, pp. 293 and 296). Another group of partial exceptions are, perhaps, those few species with very restricted ranges and very special habitat requirements, such as the mountain ringlet (*Erebia epiphron* (Knoch)).

These considerations have scarcely been given sufficient place in the two recent and important reviews of the geographical distribution of British butterflies. Beirne (1947), in his interesting attempt to reconstruct the origin and history of the British Macro-Lepidoptera, continually lays great stress on the conclusions to be drawn from the present-day ranges of the various species and minimizes the liability to alteration. He states (p. 295) that 'the majority of the interstadial [temperate period] arrivals did not move...back again as the ice-sheets [of the succeeding glacial phase]...contracted. For some reason they did not tend to recolonize a region from which they had been driven when ecological conditions there became favourable to them once more. Because of this...the extent and position of their present ranges compared with the extent and position of past ice-sheets often provide an indication of which ice-sheet was responsible for the restriction of their ranges, so that the time of their arrival may be placed at not later than the preceding interstadial phase.' Apart from the fact that, in many cases, the only evidence he brings forward to show that a species was restricted by a given glaciation is that it now has a particular southern distribution—thus arguing in a circle—this statement would seem to be very dubious as a general rule and in the particular case of the speckled wood, demonstrably misleading.

Ford (1945) is of course aware that the ranges of certain species have altered greatly in recent years, and mentions this in his discussion of the origin of the British butterfly fauna (p. 310). But it needs to be stressed that similar changes may well have occurred in the recent history of other species, where they are not, and often cannot be, precisely known. In the present paper, for example, evidence for such changes in three species, which Ford happens to have overlooked, has been given, and in each case the additional facts would involve some adjustment to the course of his argument about the history of the species in Britain. The speckled wood, the best documented case, has already been discussed. The silver-washed fritillary, it has been shown, occurred in Scotland until 1905 and it would therefore be unnecessary to introduce the supposition that it occurred there during some more remote 'warm period' of the Holocene. The large tortoiseshell also occurred in Scotland very recently, and this fact would involve its removal from Ford's Group IV (*a*) to Group IV (*b*) and might give rise to the possibility that its establishment in Britain dates from earlier than the Holocene. Were the full facts about the recent changes of range of these species known, and not only those for the last hundred years, yet another outline might have to be drawn.

The general conclusion seems rather to be that the ranges of many butterflies in Britain change so rapidly that it is difficult to derive accurate historical conclusions from a consideration of the areas occupied at the present day.

6. SUMMARY

1. At the present day the range of the speckled wood butterfly (*Pararge aegeria* (L.)) in Britain is the south and Midlands of England, Wales, and an isolated area in the west of Scotland.

2. During the nineteenth century its range was virtually continuous over England, Wales and Scotland except the extreme north.

3. From about 1860 to 1920, this larger range was greatly reduced and was divided into two widely separated parts. More recently some recovery has taken place, notably in the south of England.

4. The hypothesis that the present-day range is due to a contraction caused by a Pleistocene glaciation is untenable.

5. In addition to the speckled wood, seven other British butterflies (13% of the resident fauna) have undergone great expansions or contractions of range in the past hundred and fifty years.

6. It is suggested that this shows that the ranges of many butterflies alter so rapidly that discussion of their present ranges in Britain by the methods of classical zoogeography is very difficult.

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THE ARTHROPOD POPULATION OF PASTURE SOIL

By GEORGE SALT, F. S. J. HOLLICK, F. RAW and M. V. BRIAN
From the Zoological Laboratory, University of Cambridge

(With 1 Figure in the Text)

1. INTRODUCTION

At the time of Waksman's survey of the microfauna of the soil (1927), it had already been shown that certain animal types inhabit the soil in very large numbers. Nematodes had been reported to occur at the rate of 648 millions per acre in the upper 6 in. of a Missouri cornfield, and at an average rate of at least 338 millions per acre in fields in eight different States (Cobb, in Steiner & Heinly, 1922). Oligochaete annelids had been estimated to reach 600 millions per acre in the soil in Switzerland (Jegen, 1920).

Compared with those groups, arthropods were thought at that time to occur in the soil in rather small numbers. The densest populations of soil-inhabiting arthropods that had been reported were those studied by Morris (1922) and McAtee (1907). Morris had estimated that insects occurred at the rate of 7·7 millions per acre in an arable plot at Rothamsted; and McAtee had calculated that there were 13·6 million animals, chiefly insects, per acre in the surface soil of an American meadow.

In the twenty years that have passed since the appearance of Waksman's book, increasing attention has been paid to the soil fauna, and to the development of new methods of extracting animals from the soil. As a result, estimates of the population of soil arthropods have greatly increased. Trägårdh (1929), using Berlese funnels, studied the arthropod fauna inhabiting moss, decaying leaves, and the superficial layers of the soil in Swedish forests, and found numbers up to 51,500 per kg. of dry material. Ladell (1936) developed a flotation method, and recorded observations which indicated the existence of 47·9 million insects per acre in fallow land, and 95·6 million per acre under new grass. In experimental plots at Rothamsted, Baweja (1939, Table 7) found a mean population of the order of 105 million insects per acre. In a grass field at Slough, Glasgow (1939) studied in particular four species of subterranean Onychiuridae (Collembola) which, at their peak, reached a density of 117 millions per acre. Salt & Hollick (1944) used a benzene-water interface to separate wireworms and other arthropods from vegetation, and mentioned finding Collembola and mites at the rates of 164 and 218 millions per acre respectively. The densest population of soil insects hitherto recorded appears to be that of Ford (1935), who estimated that there were 244·8 million insects per acre in an Oxfordshire meadow.

The present paper records an attempt to estimate the arthropod population of the soil of an ordinary pasture in agricultural use. The work was done as a diversion in the course of a more pressing investigation of wireworms, and is deficient in two major respects. First, the apparatus and method used were designed for wireworms and did not serve to collect the entire population of some of the smaller forms. Secondly, no attempt has been made to identify all of the several thousands of individuals collected, which have for the most part been classified only into Orders. In spite of these failings, the work was done on a scale that cannot often be repeated, and we publish an imperfect study rather than leave the information it contains unavailable to other workers.

2. SITE AND METHODS

The field to which our estimates refer, Spinney Pasture, is a grass field of about 8 acres situated on the University Farm, 2 miles north-west of Cambridge. It has been continuously under grass for at least 10 years and is principally used for grazing although occasionally it is cut for hay. An account of Spinney Pasture, with regard to its location, topography, soil, flora, and fauna, has been given in another paper (Salt & Hollick, 1946), to which reference can be made for details.

Within this field, 20 stations were established in the positions shown on the map (Fig. 1), and a soil sample was taken near each station every month from January 1942 until April 1944. From most of those samples only wireworms and a few other animals were collected, but from the two sets of 20 samples taken on 27 May and 26 November 1943 an attempt was made to collect the whole arthropod fauna. The May collection lacks a great many of the smaller forms, especially Collembola and mites. The November collection, although very imperfect, is much more nearly complete, and it is this that provides the principal material for the present paper.

The samples taken on each occasion consisted of cylinders of soil, 4 in. in diameter and 12 in. deep. They were obtained by means of a boring tool which

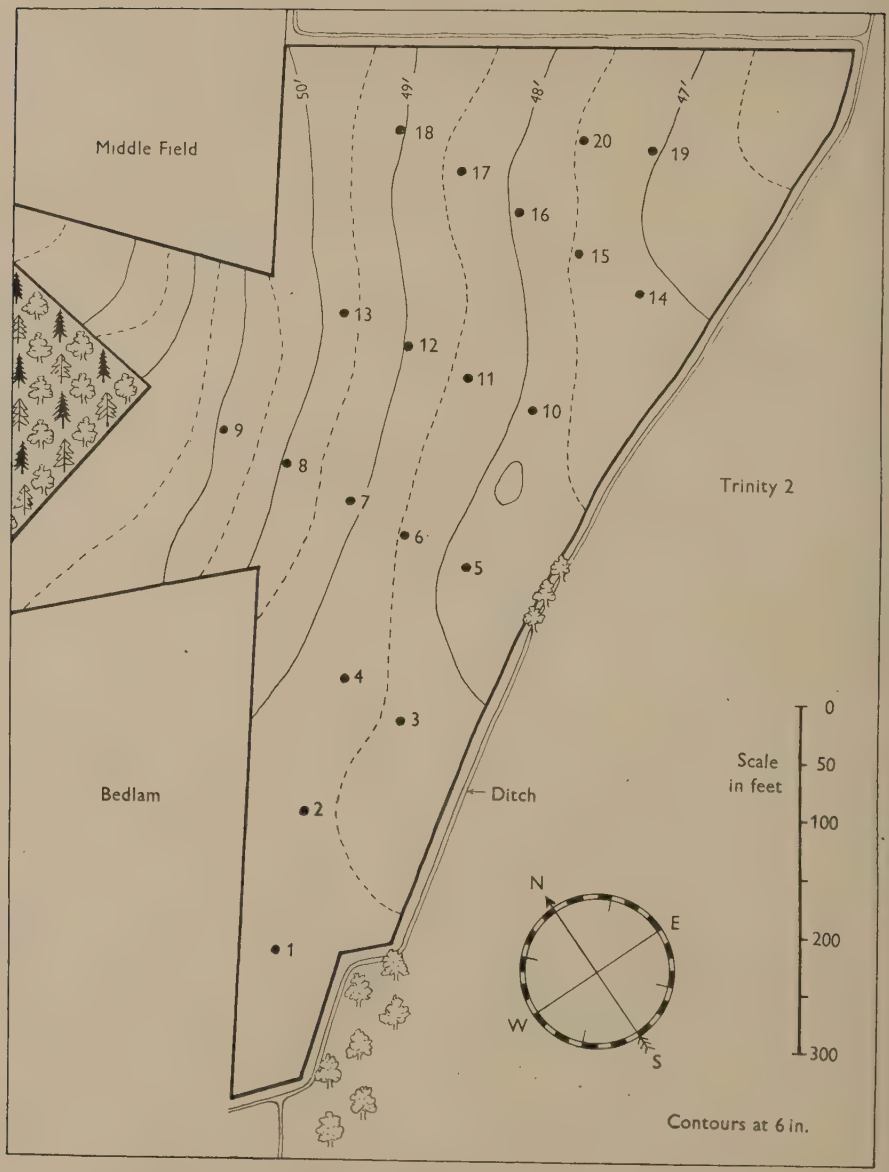

Fig. 1. Map of Spinney Pasture, showing the positions of twenty stations.

cuts and removes a core of soil 4 in. in diameter and 6 in. deep. By reinserting the tool into the hole thus formed, a second core of the same size can be removed from lower down. The two cores forming each sample were always examined separately, so as to show what part of the fauna was above and what part below a depth of 6 in. The area of a sample 4 in. in diameter is 12·6 sq.in. or 81·1 sq.cm. The volume of one sample, from the surface to a depth of 12 in., is 150·8 cu.in. or 2471 c.c.

Before taking each sample, we cut off the growing vegetation close to the surface of the ground with scissors. This practice limited the vegetation in the upper cores to the roots and basal parts of the plants, with comparatively little green material. It also disturbed some of the animals living above ground and gave them an opportunity to escape. In this manner, a good many of the surface dwellers, though by no means all, were eliminated.

The method used for removing the arthropods from the soil has been described elsewhere (Salt & Hollick, 1944). It consists essentially of the following processes. The soil samples, collected into tins, are covered with water and frozen at $-12°$ C. for at least 48 hr. After being thawed, the soil is broken apart by jets of water and the particles pass through a series of sieves, of which the coarsest retains long roots and stones, while the finest allows the escape of minute particles of clay. The long roots are pulled apart and washed under powerful jets of water in order to free any adherent animals, and are then discarded. The particulated sample is drained and at once flooded with a solution of magnesium sulphate having a specific gravity of 1·2, in which it is thoroughly stirred both mechanically and by compressed air bubbling up through it. The arthropods and other organic material float in this solution; the soil and heavy matter sinks. A process of decantation collects the floating material which, after being washed, is shaken vigorously in a mixture of water and benzene. The chitinous integument of the arthropods is wetted by the benzene and they enter the benzene layer; other material, including most of the vegetation, is not wetted by benzene and remains in the water layer. When the mixture settles, the arthropod material is found lying conspicuously on the benzene-water interface, whence it can be collected by a variety of means.

This method was originally developed with special reference to small wireworms, that is for animals at least 2 mm. long and 0·2 mm. in diameter, and was not designed for things so small as nymphal Collembola and mites. It was used unmodified for all of the May samples and for the first five November samples. We then noticed that small elements of the fauna were passing through the copper sieve, which has a square mesh 0·2 mm. across, and we added a component which filtered all the overflow water through a sieve of old bolting-silk having a mesh about 0·1 mm. across but with the holes considerably distorted. As a result of this addition, samples 6–11 inclusive yielded 1315 mites, 261 Collembola and 42 other forms, an average of 270 animals per sample, which would otherwise have been lost. Beginning with the twelfth sample we were able to use new bolting-silk with a very regular mesh of 0·1 mm. The collection from the overflow immediately rose, and from the remaining samples, 12–20, it numbered 12,941, an average of 1438 animals per sample, composed of 1141 mites, 264 Collembola and 33 others, almost exclusively pauropods and Protura.

From this account it will be clear that we make no claim to have collected all the arthropods even from the twenty November samples. If, as might be assumed, the overflow water from samples 1–11 contained the same density of animals as that from samples 12–20, our loss from the first eleven November samples can be estimated as 14,198 individuals—1438 from each of samples 1–5 and 1168 from each of samples 6–11. We regret this estimated loss, which amounts to one-third as many arthropods as we actually collected from the November samples, but we point out in extenuation that the whole of this work was a gratuitous digression from the wireworm investigations on which we were really engaged.

3. THE NOVEMBER COLLECTIONS

The numbers of arthropods of different groups that we actually collected from each of the 20 samples of November 1943 are set out in Table 1, which is therefore both the principal result of our efforts and the kernel of this paper. It can be seen that we found a total of 42,753 arthropods, of which 15,170 were insects and 26,652 were mites—an average of 2137 arthropods per sample.

In order to make these collections readily comparable with others based upon a different number or size of samples, the numbers in Table 1 must be brought to a common unit of area. The total area occupied by our 20 samples was 251·3 sq.in (1621·5 sq.cm.), and it would seem that the number per square metre would be a useful measurement for animals of this size. Most published data, however, although based on the examination of less soil than we used, are expressed as the number of individuals per acre. In Table 2, therefore, we record the density of each group per square metre and per acre and, to make the table more useful, we separate the animals found in the upper and lower cores so as to give some indication of the vertical distribution of different groups.

The arthropod population of Spinney Pasture, as represented by these collections of November 1943,

Table 1. *Numbers of arthropods collected from 20 soil samples taken in Spinney Pasture on 26 November 1943*

Station	Thysanura	Protura	Collembola	Psocoptera	Thysanoptera	Hemiptera	Lepidoptera	Coleoptera	Hymenoptera	Diptera	Total insects	Araneida	Chelonethida	Acarina	Diplopoda	Pauropoda	Symphyla	Chilopoda	Total arthropods
1	4	—	474	—	3	46	—	8	—	10	545	—	—	293	—	—	63	—	901
2	—	—	1,322	—	13	17	—	15	—	6	1,373	—	—	662	—	—	33	7	2,075
3	280	—	222	—	2	59	1	41	1	6	612	—	1	809	4	—	20	5	1,451
4	149	—	603	1	7	106	—	27	2	3	898	—	2	981	4	—	27	11	1,923
5	14	—	123	—	2	56	1	43	3	8	250	5	3	1,165	3	—	8	9	1,443
6	9	26	550	1	10	268	1	34	1	1	901	1	—	954	—	—	66	2	1,924
7	9	1	686	4	2	172	—	33	1	3	911	—	—	1,018	3	—	46	6	1,984
8	107	—	168	1	2	250	—	46	—	3	577	1	—	1,455	2	—	16	3	2,054
9	144	—	250	3	4	222	1	46	—	36	706	—	—	691	3	—	20	5	1,425
10	17	7	215	1	8	353	—	22	—	3	626	—	1	394	1	—	21	3	1,046
11	45	2	316	1	9	68	2	47	—	11	501	2	—	1,171	5	—	31	12	1,722
12	4	—	299	3	4	126	—	18	—	3	457	1	—	2,322	6	—	48	3	2,837
13	—	—	280	1	6	142	—	14	—	4	447	—	—	1,302	—	6	54	2	1,811
14	76	123	573	1	25	138	—	42	1	—	979	2	—	1,184	5	3	37	10	2,220
15	5	34	354	—	13	117	1	43	—	2	569	1	—	1,462	2	—	26	—	2,060
16	50	—	603	3	38	147	1	54	—	2	898	1	—	3,662	10	36	27	8	4,642
17	25	1	395	—	10	79	—	44	—	2	556	—	—	2,714	4	34	23	8	3,339
18	32	—	776	1	7	95	1	36	—	3	951	2	—	1,349	4	13	14	2	2,335
19	17	2	573	2	15	97	—	38	—	1	745	6	—	1,858	4	4	30	5	2,652
20	84	25	1,153	—	3	316	1	62	22	2	1,668	1	2	1,206	5	6	17	4	2,909
Total	1,071	221	9,935	23	183	2,874	10	713	31	109	15,170	23	9	26,652	65	102	627	105	42,753

Table 2. *Number and density of arthropods collected from upper and lower cores and whole samples taken in Spinney Pasture on 26 November 1943*

	Upper cores			Lower cores			Whole samples		
	No. collected	Density per sq.m.	Density in thousands per acre	No. collected	Density per sq.m.	Density in thousands per acre	No. collected	Density per sq.m.	Density in thousands per acre
Thysanura	599	3,694	14,975	472	2,911	11,800	1,071	6,605	26,775
Protura	44	271	1,100	177	1,092	4,425	221	1,363	5,525
Collembola	6,989	43,101	174,725	2,946	18,168	73,650	9,935	61,269	248,375
Psocoptera	12	74	300	11	68	275	23	142	575
Thysanoptera	175	1,079	4,375	8	49	200	183	1,129	4,575
Hemiptera	2,466	15,208	61,650	408	2,516	10,200	2,874	17,724	71,850
Lepidoptera	9	56	225	1	6	25	10	62	250
Coleoptera	455	2,806	11,375	258	1,591	6,450	713	4,397	17,825
Hymenoptera	28	173	700	3	19	75	31	191	775
Diptera	84	518	2,100	25	154	625	109	672	2,725
Total insects	10,861	66,980	271,525	4,309	26,574	107,725	15,170	93,553	379,250
Araneida	23	142	575	—	—	—	23	142	575
Chelonethida	3	19	75	6	37	150	9	56	225
Acarina	19,420	119,763	485,500	7,232	44,600	180,800	26,652	164,363	666,300
Diplopoda	26	160	650	39	241	975	65	401	1,625
Pauropoda	5	31	125	97	598	2,425	102	629	2,550
Symphyla	43	265	1,075	584	3,602	14,600	627	3,867	15,675
Chilopoda	35	216	875	70	432	1,750	105	648	2,625
Total arthropods	30,416	187,575	760,400	12,337	76,082	308,425	42,753	263,658	1,068,825

was 263,658 per square metre, or 1068 millions per acre. Mites, with a density of 164,000 per square metre, constituted 62% of the population; Collembola, with 61,000 per square metre, were the next most numerous group; and these two so much outnumbered all others that together they made up six-sevenths of the arthropod population. In these collections, Hemiptera were the only other arthropods having a density greater than 10,000 per square metre, but, as will be shown below, their occurrence at that rate may have been a seasonal phenomenon.

4. THE MAY COLLECTIONS

The 20 soil samples collected on 27 May 1943 were examined by the ordinary method used for wireworms, without the introduction of any sieve finer than that of 0·2 mm. mesh. Our experience with the November samples, described above, indicates that there must have been a considerable loss of the smaller animals. It is likely, however, that the collections of the larger forms are complete, and on that account we record our collections from these samples in Table 3.

This record of the collections of 27 May is chiefly useful for the comparison it allows with the collections of six months later. So far as the larger forms are concerned, the method used for examining the soil samples should have been equally efficient in the two cases. It is therefore interesting, and reassuring, to find that the numbers of Lepidoptera, Hymenoptera, Diptera, spiders and Diplopoda are almost exactly the same in the two collections, and the numbers of Thysanoptera and Coleoptera are of the same order. It is likely, also, that the Thysanura, Psocoptera and Symphyla were present in much the same numbers, for the column labelled 'miscellaneous' in Table 3 contains a number of individuals similar to the sum of those three groups in Table 1, and cannot include many Protura or pauropods because those forms were caught in numbers in November only when the 0·1 mm. sieve was added. Since many Collembola and Acarina must have passed through the 0·2 mm. mesh in May, as they were found to do in November, the numbers of these two groups shown in Table 3 are naturally a good deal lower than those in Table 1. Only two groups, the Chilopoda and Hemiptera, call for explanation. The former were half as numerous in May as in November, a difference that seems to be real ($t = 3{\cdot}45$, 1% value 2·86 for 19 degrees of freedom) but perhaps requires larger numbers to be biologically convincing. The Hemiptera show a very large change, being nine times as numerous in November as in May. This probably represents a real change in population, for comparison of the two collections shows a highly significant difference ($t = 6{\cdot}55$; 1% value 2·86 for 19 D.F.).

Table 3. *Numbers of arthropods collected from 20 soil samples taken in Spinney Pasture on 27 May 1943*

Station	Collembola	Thysanoptera	Hemiptera	Lepidoptera	Coleoptera	Hymenoptera	Diptera	Araneida	Acarina	Diplopoda	Chilopoda	*Miscellaneous	Total arthropods
1	178	3	2	—	16	—	5		273	—	—	61	538
2	696	2	5	—	22	—	3	3	255	—	1	61	1,048
3	567	—	6	—	19	1	1	—	243	2	—	80	919
4	710	4	6	1	22	—	48	—	570	4	1	102	1,468
5	577	2	24	—	54	6	3	1	521	6	5	107	1,306
6	493	—	52	1	51	—	5	—	544	3	3	122	1,274
7	670	2	1	1	21	—	1	—	440	3	3	97	1,239
8	221	3	9	—	11	1	3	—	373	2	1	51	675
9	312	1	17	1	24	2	3	3	338	—	3	74	778
10	205	7	33	1	26	1	7	—	487	—	1	48	816
11	49	2	14	1	35	11	2	3	354	6	3	58	538
12	449	3	3	—	27	1	3	4	383	2	4	121	1,000
13	101	1	7	—	20	—	2	—	275	—	3	45	454
14	246	37	7	1	25	2	8	6	840	3	6	44	1,225
15	179	8	14	—	19	—	4	—	479	4	2	85	794
16	219	10	25	—	36	1	5	4	485	13	5	96	899
17	171	3	15	2	40	1	1	—	341	2	2	100	678
18	123	12	35	—	24	1	1	3	437	2	3	44	685
19	111	23	13	1	21	—	7	1	565	8	4	83	837
20	283	27	25	—	36	5	3	1	504	8	3	84	979
Total	6,560	150	313	10	549	33	115	29	8,707	68	53	1,563	18,150

* This column includes members of the Thysanura, Protura, Psocoptera, Pauropoda and Symphyla, which were not separately recorded.

5. NOTES ON THE FAUNA

The following notes on the fauna refer exclusively to the November collections except where those of May are specifically mentioned.

Thysanura. The collections consist mainly, probably entirely, of a single species, *Campodea staphylinus* Westw. Specimens range in length from 1·6 to 3·2 mm., with head capsules between 0·4 and 0·6 mm. broad. This size ensures that no individuals were lost through the 0·2 mm. sieve, and the collections from all 20 stations can be considered complete. The twenty collections are conspicuously unequal in number, and statistical analysis confirms that the Thysanura were markedly aggregated. The factors that determined this distribution must operate through the top 12 in. of soil, and not separately in the upper and lower cores, for the numbers in the two cores of each sample are significantly correlated ($r = +0{\cdot}851$; 1 % pt. 0·561 for 18 D.F.).

Protura. This group appears to be represented by a single species of the family Acerentomidae, measuring 0·5–0·7 mm. in length and 0·1 mm. in maximum breadth. These animals are so small that many may have been lost and, indeed, we could not expect to have found any that were in the first five samples, before the bolting-silk sieve was added. The collections from samples 6–20 are curiously limited to stations at the lower, south-eastern end of each row, but the coefficient of correlation, for what it is worth, between number of Protura and station altitude just fails to reach the level of significance ($r = -0{\cdot}502$; 5 % pt. 0·514 for 13 D.F.). The Protura collected from the lower cores were four times as numerous as those found in the upper cores, but the difference is not significant ($t = 1{\cdot}359$; 5 % pt. 2·145 for 14 D.F.).

Collembola. This group is represented at Spinney Pasture by 26 species, as shown in the following list. The number in brackets following each name indicates the number of individuals of that species found in the November collections from stations 12–20; the collections from the other stations, being incomplete, were not wholly identified. The species marked with an asterisk belong to the hypogeal fauna.

Sminthuridae
- *Sminthurus viridis* L. (0)
- *Sminthurides malmgreni* Tlbg. (1)
- *S. schotti* Axels. (124)

Mydonidae
- *Lepidocyrtus cyaneus* Tlbg. (808)
- *L. anglicanus* Jacks. (37)
- *L. rivularis* Bourl. (4)

Sinella curviseta Brook (141)
Mydonius marginatus Tlbg. (15)
M. nivalis f. *principalis* L. (2)
M. multifasciatus Tlbg. (1)
Orchesella villosa L. (10)

Isotomidae
**Isotomiella minor* Schffr. (55)
Spinisotoma ephippiata Brian (0)
Parisotoma delicatula Brown (98)
P. notabilis Schffr. (56)
Isotoma olivacea Tlbg. var. *grisea* Lubb. (18)
I. viridis Bourl. (102)
Pseudoisotoma sensibilis Tlbg. (2)
Folsomia fimetaria L. (2)

Achorutidae
**Achorutes armatus* Nic. (94)

Neanuridae
**Macgillivraya mirabilis* Tlbg. (387)

Onychiuridae
**Onychiurus fimetarius* L. Lubb. (17)
**Protaphorura armata* Tlbg. (120)
**P. alborufescens* Vogl. (1347)

Tulbergidae
**Stenaphorura denisi* Bagn. (191)
**Mesaphorura krausbaueri* Börn. (1226)

Some of the species of Collembola found at Spinney Pasture are so small that they could pass readily through the 0·2 mm. sieve and were therefore not completely collected from samples 1–11. Indeed, of the total of 5006 Collembola collected from samples 12–20, 2375 were found in the component filtering the overflow water through bolting-silk of 0·1 mm. mesh. We can be sure, therefore, that the figure of 61,000 per sq.m., or 248 million per acre, indicated by the twenty November collections, is far less than the population actually present. The figure of 68,604 per sq.m., or 278 millions per acre, indicated by samples 12–20 alone, is probably a closer estimate. The maximum density found in our samples was in the top core of station 2, where there were 1036 individuals, which is 838 Collembola per litre, or 1 Collembolan per 1·2 c.c. of soil.

A more detailed account of these collections of Collembola will be published separately by M. V. Brian.

Thysanoptera. Thrips do not belong to the subterranean fauna, and of the 183 collected, 175 were found in the upper cores. The other 8 probably fell into the hole formed by the removal of the upper core, and were then collected with the lower soil.

Hemiptera. The 2874 Hemiptera collected from the November samples, as well as the 313 from the May samples, consist almost exclusively of root aphids. They have been handed to Mr A. W. Colling, who intends to study them thoroughly and to publish a separate paper on them. He informs us that the vast majority represent a single species, *Tycheoides eragrostidis* Pass., which is known to feed on the roots of grasses.

Coleoptera. Of the 713 Coleoptera collected from the November samples, 471 were wireworms of the genus *Agriotes*, almost exclusively *A. sputator* (L.). The remaining 242 Coleoptera included 41 larval and 109 adult Staphylinidae together with 61 larvae and 31 adults of other families. The beetles collected in May amounted to 549, made up as follows: *Agriotes*, 350; Staphylinidae, 54 larvae and 73 adults; other families, 53 larvae and 19 adults.

The Rev. C. E. Tottenham has been so good as to examine the adult beetles, other than *Agriotes*, from these two collections. Since many of the specimens submitted to him were broken or represented only by parts, Mr Tottenham was unable to identify all of the 232 individuals precisely, but, with a patience for which we are grateful, was able to put names on 184 of them, representing at least 33 species. The number of individuals of each species is shown in the following list separately for the May and November collections, together with their distribution at the twenty stations on the field.

	May	November	Stations
Carabidae			
Clivina fossor Linn.	1	—	12
Bembidion obtusum Serv.	1	2	5, 7, 15
Trechus sp.	1	—	8
Microlestes maurus Sturm	3	15	3, 4, 5, 11, 16, 19
Hydrophilidae			
Helophorus brevipalpis Bedel	—	1	10
Cercyon sp.	1	—	2
Staphylinidae			
Oxytelus sculpturatus Grav.	3	1	8, 16
O. inustus Grav.	1	—	15
Euaesthetus bipunctatus Ljungh	—	1	11
Stenus brunnipes Steph.	3	—	11
Sunius propinquus Brisout	5	8	5, 8, 11, 14, 15, 16, 17, 18
Lathrobium fulvipenne Grav.	1	3	4, 5, 15
L. longulum Grav.	—	2	14, 18
Achenium sp.	—	1	5
Xantholinus linearis Oliv.	1	2	9, 17

Staphylinidae (*cont.*)	May	November	Stations
Quedius semiobscurus Marsh.	1	—	4
Tachyporus hypnorum Fabr.	—	5	4, 5, 10, 19
T. chrysomelinus Linn.	—	2	16, 19
T. nitidulus Fabr.	—	8	5, 9, 16
T. atriceps Steph.	—	1	9
T. pusillus Grav.	—	1	16
Tachyporus sp.	4	17	3, 4, 5, 6, 8, 9, 11, 12, 13, 14, 16, 18, 20
Cordalia obscura Grav.	1	—	8
Amischa sp., including *analis* Grav. and *decipiens* Sharp	19	47	3, 5, 6, 7, 8, 11, 12, 13, 15, 16, 17, 18, 19
Drusilla canaliculata Fabr.	2	1	4, 5, 11
Coccinellidae			
Micraspis 16-punctata Linn.	1	—	1
Scydmaenidae			
Stenichnus collaris Mellié	—	4	16
Lathridiidae			
Enicmus minutus Linn.	1	—	12
Cantharidae			
Malthodes sp.	1	—	5
Ptinidae			
Ptinus tectus Boiel.	—	2	12
Curculionidae			
Phyllobius viridiaeris Laich.	—	1	3
Sitona flavescens Marsh.	—	1	1
S. hispidulus Fabr.	2	2	5, 11, 17, 18
Sitona sp.	—	3	3, 8, 12

Hymenoptera. The 31 Hymenoptera of the November collections included 23 ants and 8 Parasitica, as listed below.

Formicidae
Myrmica sulcinodis Nyl. 1 worker from station 4.
Acanthomyops flavus Fabr. 1 female, 2 workers and 19 larvae, collected together in the upper core from station 20.
Mymaridae
Litus cynipseus Hal. 1 female from station 6.
Calliceratidae
Calliceras? insularis Kieff. 4 females from stations 3, 4, 7 and 14.
Diapriidae
Ashmeadopria verticillata Latr. 2 females from station 5.
Trichopria cilipes Kieff. 1 female from station 5.

The 33 Hymenoptera of the May collections included 26 ants and 7 Parasitica, as follows:

Formicidae
Myrmica laevinodis Nyl. 6 workers from stations 14, 18 and 20.
Myrmica sulcinodis Nyl. 1 female and 8 workers from stations 5, 9 and 17.
Myrmica scabrinodis Nyl. 11 workers from station 11 only.
Ichneumonidae
Cryptinae. Fragment insufficient for identification from station 8.
Mymaridae
Lymaenon sp. 1 female inside egg-shell of host from station 10.
Anaphes sp. 1 female from station 20.
Patasson crassicornis Walk. 1 female from station 12.
Pteromalidae
Cyrtogaster vulgaris Walker. 1 male from station 3.
Calliceratidae
Calliceras? nigraticeps Kieff. 1 female from station 20.
Serphidae
Exallonyx curtigena Nixon. 1 female from station 16.

The common Serphid parasite of wireworms, *Paracodrus apterogynus* Hal., is known to occur at Spinney Pasture, but was not present in either the May or November samples.

We are indebted to Mr G. E. J. Nixon of the British Museum for identifying the Proctotrypoids, and to Mr H. Britten for identifying the Mymaridae.

Diptera. Of the 109 Diptera collected, 62 were larvae belonging to the Sciarinae, 33 were other Nematocera, and 14 were cyclorrhaphous larvae.

Araneida. Spiders do not belong to the subterranean fauna. All of the 23 collected were found in the upper cores, and were probably hiding at the base of the grass stems when the samples were taken.

Acarina. The number of mites collected is so large that no thorough study of them has yet been possible; but it is hoped that one of us (F.R.) will be able to publish a more detailed account later on.

A general idea of the composition of the macroacarine fauna can be obtained from Table 4, in which a sample of 3871 mites from the November collections and 1167 from the May collections are separated into cohorts or families, following the classification of

Vitzthum (1931). In order that the two parts of the table shall be comparable, only forms collected with the 0·2 mm. sieve are included. In both months, the Oribatei were most numerous and constituted about half the population, while Acarids and Gamasids together made up most of the remainder.

Table 4. *Composition of part of the Acarine soil fauna at Spinney Pasture in May and November* 1943

	May		November	
	No.	%	No.	%
Sarcoptiformes				
Oribatei	703	60·3	1720	44·4
Acaridiae	193	16·5	484	12·5
Tyroglyphidae	32	2·7	477	12·3
Parasitiformes				
Gamasidae	189	16·2	934	24·1
Uropodina	—	—	1	—
Trombidiformes				
Tarsonemidae	—	—	15	0·4
Trombidiidae	—	—	111	2·9
Unclassified	50	4·3	129	3·3
Total	1167		3871	

In addition to this macro-acarine fauna there is a host of smaller acarines able to pass through the 0·2 mm. mesh and recovered only by use of the bolting-silk sieve. This part of the fauna, which was completely missed in the May collections, includes many larvae and small forms, and is much more difficult to study than the other. In the November sample from station 13, for instance, the micro-acarine fauna consisted of 245 small round Oribatei, 43 Tyroglyphidae, 23 nymphal Oribatids, Acarids and Gamasids, and 91 larvae of three types. The Oribatei from these collections are the smallest adult forms seen, and are so minute that only adults and nymphs were recovered, the larvae having probably passed through the 0·1 mm. sieve.

Diplopoda. The 65 millipedes of the November samples include 59 Julidae and 6 Polydesmidae. Five of the latter came from the upper cores and only one from a lower core, while of the Julidae, 21 were from the upper and 38 from the lower soil. The 68 millipedes of the May samples include 63 Julidae and 5 Polydesmidae. Three polydesmids came from upper and two from lower cores; 26 Julidae from the upper soil and 37 from the lower.

Pauropoda. These animals are so small that they passed with ease through the 0·2 mm. sieve and were collected only when the 0·1 mm. sieve was added. Indeed, it must be supposed that a good many were lost even then, for the size of specimens mounted on slides ranges from 0·8 to 1·2 mm. long but only 0·05 to 0·08 broad, so that passage through the mesh of the bolting-silk could take place fairly readily. The specimens examined appear to be referable to the species *Pauropus huxleyi* Lubbock.

Symphyla. The Symphyla in the November collections all belong to the Scolopendrellidae, and most of them to the species *Scolopendrella subnuda* Hansen. A few specimens were examined that seem to represent another species of the same genus.

Mature individuals measure 2–3 mm. in length, but immature specimens may be only 0·9 mm. long and their head capsules only 0·07 mm. across. Some of these small individuals passed through the 0·2 mm. mesh, so that of the 627 Symphyla collected, 59 were caught in the bolting-silk sieve added for the examination of samples 6–20. The numbers shown in Table 1 for stations 1–5 may, therefore, be about 10% too low.

The Symphyla are well known to be members of the really subterranean fauna, and in our collecting nearly 14 times as many were found in the lower cores as in the upper soil.

Chilopoda. Of the 105 centipedes collected in November, 99 were *Geophilus* and 6 *Lithobius*; of the 53 collected in May, 52 were *Geophilus* and only 1 *Lithobius*.

In May, 65% of the *Geophilus* (34 out of 52) were found in the upper cores; in November, only 32% (32 out of 99). The numbers are too low for a firm conclusion to be drawn, but they suggest that these truly hypogeal centipedes may move up and down in the soil at different seasons. It has already been remarked (p. 143) that the difference in numbers between the May and November collections is statistically significant.

6. DISCUSSION

The object of the present work was to estimate the arthropod population of an ordinary pasture in agricultural use. From 20 cylindrical samples of soil, 4 in. in diameter and 12 in. deep, taken on 26 November 1943, we collected 42,753 arthropods, representing a density of 263,658 per square metre or 1068·8 millions per acre. Those numbers, large as they are, do not represent a complete, let alone a maximum, population of soil arthropods. We have estimated above that the coarseness of our sieves allowed 14,198 animals to escape in the overflow from samples 1–11. If that estimated loss is added to the animals actually collected, a total of 56,951 is reached, representing an arthropod population of 1423·8 millions per acre. If, instead, we calculate the population entirely from the nine samples, 12–20, which we examined most carefully, the estimate becomes 1378 million arthropods per acre, including 948 million mites and 280 million Collembola. But even these figures are incomplete, for we know that loss of small forms between 0·1 and 0·2 mm. in diameter

could and probably did take place among the clay in the settling tanks; and anything having a diameter of less than 0·1 mm. could pass freely through our finest sieve. The density of soil arthropods indicated by this November collection is much larger than has hitherto been published, but it is still below that which we must expect to find.

On the scale of millions per acre, or even thousands per square metre, the arthropod population of the soil is difficult to visualize, and a more realistic view of the soil fauna can be had if the density of population is described in other terms. The volume of one sample of soil 4 in. in diameter and 12 in. deep is 150·8 cu.in., or 2471 c.c. The average population of all our samples was 2137 arthropods. If they had been distributed regularly throughout the soil, the animals would have occurred at a density of 14 per cu.in., or just under 1 per c.c. of soil. Of course, they were not so distributed; there were far more in the upper than in the lower cores. Taking for another estimate the number of arthropods in the upper cores of samples 12–20, we have 16,599 in 678·6 cu.in., which is a density of 24 per cu.in., or 1·5 per c.c. The maximum density found by us was in the upper core of station 16, where there were 3771 arthropods in 75·4 cu.in., which is 50 per cu.in., or 3 per c.c.

But it is difficult to picture even one animal per c.c. when the range of size of the animals concerned is so great as that of the soil arthropods. The smallest animals we collected were those which, having passed through a sieve of 0·2 mm. mesh, were caught on a sieve of 0·1 mm. mesh. Among them, some of the mites approximate a spherical shape and can be calculated to have a volume of between 5×10^{-7} and 4×10^{-8} c.c. The largest arthropods present in our collections in any numbers were large wireworms, which have an average volume of about 0·05 c.c. Such a range of size prohibits any immediate visualization of a representative arthropod in the soil for, at a rate of one individual per c.c. of soil, the wireworm would occupy one-twentieth of its spatial environment, the mite only one part in two million.

This difficulty leads us to consider the size of soil arthropods in relation to their numbers. We find that in two respects the smaller ones greatly outnumber the larger. First, taking a particular species, it has already been shown (Salt & Hollick, 1944) that in a population of wireworms inhabiting pasture there are large numbers of small larvae in the earlier instars and gradually decreasing numbers of large larvae in the later instars. Although it has not been formally demonstrated, this structure of the population can be assumed from theoretical grounds to occur among other members of the soil fauna. It is undoubtedly true of the Hemiptera and Symphyla collected from the November samples, for the great majority of the soil aphids were small, immature individuals, and Symphyla having the adult complement of legs were comparatively scarce.

Secondly, taking the fauna as a whole, it is very noticeable that the smaller types of arthropods are much more numerous than the larger. There were in our November collections about 27,000 of the smallest arthropods, the Acarina, Protura and Pauropoda. Forms of the size of Collembola, Psocoptera and Thysanoptera numbered roughly 10,000. The soil aphids, Thysanura and Symphyla came to nearly 4500. All the others, ranging from small beetles such as the Staphylinidae and their larvae to large wireworms, millipedes and centipedes, reached a total of about 1000. The Orders and Classes mentioned in each of these groups are to be understood to represent merely the order of size, for in all of them the size of different species, and of different individuals of one species, naturally varies a good deal. Some mites are larger than small Collembola and some Symphyla are smaller than large Collembola. But there can be no doubt that the arthropod fauna as a whole shows a marked inverse correlation between the size of the individuals and their number.

For both of these reasons, if an attempt is made to visualize the spacing of the arthropod fauna of the soil, an animal belonging to the smaller size groups must be had in mind. Our impression, from making and studying the collections described in this paper, is that an animal having a volume of about 5×10^{-5} c.c. might be considered about average among all the individuals collected. If that estimate be accepted, the arthropod fauna of the soil occupies about one part in twenty thousand of the gross space in which it lives. This is a much greater proportion than has been estimated (cf. Lotka, 1925, p. 174) to be occupied by the micro-organisms in the sea.

The horizontal distribution of wireworms has been shown (Salt & Hollick, 1946) to be non-random and aggregated; and it is a matter of some ecological interest to discover whether some of the other groups of soil arthropods are similarly distributed. Coefficients of dispersion have been calculated on the twenty November collections of Thysanura, Hemiptera, Coleoptera, Diptera, Symphyla and Chilopoda, and on the nine collections (from stations 12–20) of Protura, Collembola and Acarina. They have also been calculated for the twenty May collections of Collembola, Hemiptera, Coleoptera, Diptera and Acarina; that is, for all groups truly soil-dwelling of which the numbers are large. In every case the coefficients are significantly greater than unity. So far as these collections go, then, and so far as this statistical test is valid, it appears that a non-random, aggregated distribution is common to several groups of soil arthropods.

Some idea of the vertical distribution of different groups can be obtained from Table 2, where it appears

that the Collembola, Hemiptera, Coleoptera and Acarina, although numerous in the lower cores, are commoner in the soil above 6 in. depth. The Protura, Pauropoda and Symphyla, on the other hand, were collected in larger numbers from the soil between 6 and 12 in. deep.

In the case of the Collembola and Acarina, groups including many species and showing a considerable range of size, it appears that the larger forms live near the surface and the smaller forms lower down. This is most easily shown in our material by comparing the collections made from stations 12–20 by the sieves of 0·2 and 0·1 mm. mesh. If the animals retained by the coarser sieve are accepted as large and those by the finer sieve as small, the collections from the upper and lower cores can be divided in a manner summarized in Table 5. The proportion of large forms is there seen to be almost invariably higher in the upper soil (one exception in 17 cases); and the mean difference for the nine samples in the case of the Collembola and eight samples in the case of the Acarina is highly significant. We realize that the sorting process in our sieves may be imperfect, but the fact is sufficiently clear that within these groups the smaller forms lived deeper in the soil.

Table 5. *Preponderance of large forms of Collembola and Acarina in the upper cores and of small forms in the lower cores of samples* 12–20

	Percentage[1] of large forms					
	Collembola			Acarina		
Station	Upper soil	Lower soil	Difference	Upper soil	Lower soil	Difference
12	69	22	47	40	8	32
13	71	25	46	62	18	44
14	43	57	−14	[56]	Lost	—
15	89	45	44	40	15	25
16	73	52	21	61	18	43
17	80	39	41	40	9	31
18	30	21	9	50	16	34
19	66	19	47	50	16	34
20	62	43	19	62	21	41
Means	64·8	35·9	29	50·6	15·1	35·5
t			4·04**			15·2**
	1 % level, 8 D.F., $t=3·355$			1 % level, 7 D.F., $t=3·499$		

[1] The total numbers involved are: Collembola, 5006 (upper soil, 3427; lower soil, 1579); Acarina, 17,059 (upper soil, 11,408; lower soil, 5651).

** Significant at 1 % level.

It was no part of our object to look for rare arthropods in the soil, but it is perhaps worth mentioning that the November collections contained representatives of one Class (Pauropoda), two Orders (Thysanura and Protura), one Family (Symphyla, Scolopendrellidae), and several genera and species that are not included in the most recent list of the fauna of Cambridgeshire (Imms, 1938). Moreover, some of those animals, known to many zoologists only in textbooks, occurred in the soil of Spinney Pasture in considerable numbers; the Scolopendrellidae, for instance, rather uniformly at a rate of nearly 4000 per square metre.

It would be a natural end of this discussion to compare our estimates of the arthropod population of the soil with other published data. Much as we should like to contrast the soil population of grassland with that of cultivated fields or forests, or the numbers found in England with those in other parts of the world, it would be futile, if not positively misleading, to do so at present. It is no disparagement of the pioneer efforts of 20 years ago to say that the numbers then recorded are so palpably incomplete as to give no sure ground for comparison; and in some more recent work the methods of sampling are so different from ours as to afford no common unit.

Only two investigations allow useful comparison; both are of grassland; and with both a considerable agreement in numbers is to be found. Glasgow (1939, p. 343) records a maximum population of 117 millions per acre of four species of Onychiuridae and Tullbergidae in a grass field at Slough. Five species of these families occurred in our samples 12–20 at a rate of 160 millions per acre. Ford (1936) reports an average population of soil Collembola of 244 millions per acre, basing his estimate on two or three samples a month taken in six months. Our figure for 20 samples taken in one month is 248 millions per acre. Although they were based on quite different methods of sampling and examination, these estimates are so close that we can begin to think that we know the

order of magnitude of the Collembolan population of English grassland. But comparable data for arable fields, for woods or moors, for different soil types, and from different regions of the world remain to be accumulated.

7. ACKNOWLEDGEMENTS

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8. SUMMARY

1. From 20 samples of soil, each 4 in. diameter and 12 in. deep, collected on 26 November 1943 from a pasture near Cambridge, there were extracted 42,753 arthropods (Table 1), representing a population of 263·6 thousands per sq. metre, or 1068·8 millions per acre.

2. The collection is known to be incomplete, chiefly by loss of small Acarina, and it is estimated that the complete arthropod population was at least 1400 millions per acre.

3. The collections of the principal arthropod groups, and the populations they represent, are set out in Table 2.

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THE DISTRIBUTION OF WILD DEER IN ENGLAND AND WALES

By W. L. TAYLOR, *Forestry Commission*

(With Map)

In 1938 a list of deer populations in the Forestry Commission's areas in England and Wales was compiled from observations made, by the Forest Officers and Foresters concerned, over the period 1919–38 (Taylor, 1939). It is possibly of interest to record the results of a census taken 10 years later (1948) with the co-operation of the Commissioners' Directors of Forestry for England and for Wales and field staffs in these countries, for whose interest and assistance I am greatly indebted. As previously, the present list does not purport to be an exhaustive record of the existing distribution of the various species which are found running wild to the south of the Scottish Border, but rather to show the widespread area over which various species of deer occur and to give indication of their local densities.

In accordance with Forest Policy the Commissioners' programme is an expanding one. A number of additional forest areas have been acquired in the past 10 years, in some of which the presence of deer is now reported for the first time. These newer forests have been added to the 1938 list and are indicated by means of an asterisk.

No additional species appear to have acclimatized themselves in the State forests during the decade. Siberian roe (*Capreolus pygargus*) shows a definite restriction of range; Japanese deer (*Sika nippon*) are now reported from Puddletown, Dorset, otherwise this species seems to have maintained itself in its previously adopted stations; and Chinese muntjac (*Muntiacus reevesi*) has taken up residence at Hazelborough and Yardley Chase in Northamptonshire. The last-mentioned species suffered heavily during the severe winter of 1946–7 and numbers died. At Buriton Forest, Hampshire (previously scheduled under Sussex), more than one species were reported in 1938 but they were not identified. The 1948 report mentions fallow deer (*Dama dama*) only, but it is possible that roe (*Capreolus capreolus*) are occasionally seen. In general the identifications may be accepted as reliable, but, in regard to densities, it is not certain that confusion in classification has not sometimes arisen between 'not numerous' and 'occasional'.

The effects of the past 10 years on deer populations are not everywhere easy to assess. The clear felling of woods, the more intensive interest in agriculture, precautions against foot-and-mouth disease, and, in some cases, the proximity of military camps, have tended to reduce numbers in several parts of the country. The shortage of butchers' meat has also had its effects in some districts. In other localities the preoccupations of the war years have had an opposite influence and, left to themselves, the deer have increased, both in numbers and range. Although the evidence remains conclusive that deer, in a wild state, are widely spread in England, it is also clear that this is not the case in Wales, where singularly few indications of wild deer have yet been observed. Reports from the majority of Welsh forest areas state categorically that no deer exist therein, while deer reported as 'occasional' in forests in the counties of Caernarvon, Merioneth and Montgomery in 1938 appear to have failed to perpetuate themselves in these stations.

Where wild deer become so numerous as to be damaging to young plantations, numbers are, of necessity, kept in check in the Forestry Commission's forests, a check that is also necessary in some forests in the interests of adjacent farms; but it is not possible to destroy deer to the point of extermination in extensive woodland without entirely disproportionate effort, especially where infiltrations of new blood repeatedly take place from the surrounding countryside. Roe deer (*Capreolus capreolus*) are reported from eleven new stations, and it may be assumed, with some degree of certainty, that the species is enabled to establish itself more widely as new covert is provided by afforestation.

In Table 1, column 4 restates the densities assessed in 1938, those for 1948 being shown in column 5.

England and Wales
NORTHUMBERLAND
CUMBERLAND
DURHAM
WESTMORLAND
NORTH RISING
YORK
EAST RIDING
WEST RIDING
LANCASHIRE
ISLE OF MAN
ANGLESEY
CHESHIRE
FLINT
DENBIGH
CARNARVON
MERIONETH
MONTGOMERY
DERBY
NOTTINGHAM
LINCOLN
STAFFORD
SALOP
LEICESTER
RUTLAND
NORFOLK
CAMBRIDGE
HUNTINGDON
SUFFOLK
CARDIGAN
RADNOR
BRECKNOCK
HEREFORD
WORCESTER
WARWICK
NORTHAMPTON
BEDFORD
PEMBROKE
CARMARTHEN
GLAMORGAN
MONMOUTH
GLOUCESTER
OXFORD
BUCKINGHAM
HERTS
ESSEX
MIDDLESEX
LONDON
WILTS
BERKS
SURREY
KENT
SOMERSET
HANTS
SUSSEX
DEVON
DORSET
I.W
CORNWALL
Scale
10 0 20 40 60 80 100 Miles

Table 1

1	2 Forest		3	4	5
County	No.	Name	Species	Density 1938	Density 1948
Northumberland	1	Kielder	Roe	Numerous	Not numerous
	2	Redesdale	,,	Not numerous	,, ,,
	3	Tarset*	,,	—	,, ,,
	4	Warke*	,,	—	,, ,,
	5	Slaley*	,,	—	Occasional
	6	Swarland*	,,	—	,,
	7	Harwood	,,	Numerous	Not numerous
	8	Rothbury	,,	,,	,, ,,
		,,	Fallow	Not numerous	None observed
Cumberland	9	Kershope	Roe	,, ,,	Numerous
	10	Blengdale*	,,	—	Occasional
	11	Greystoke*	,,	—	,,
	12	Thornthwaite*	,,	—	,,
Durham	13	Chopwell	,,	Not numerous	Not numerous
	14	Hamsterley	,,	(None reported)	,, ,,
		,,	Red	,, ,,	Occasional
		,,	Fallow	Occasional	None observed
Lancashire	15	Grizedale	Red	Numerous	Numerous
(Furness)		,,	Fallow	(None reported)	Occasional
		,,	Roe	Numerous	,,
	16	Broughton Moor*	,,	—	,,
Yorkshire	17	Allerston	Fallow	Occasional	,,
		,,	Red	(None reported)	,,
	18	Sproxton*	,,	—	Not numerous
	19	Cropton*	,,	—	Occasional
	20	Wykeham*	,,	—	,,
	21	Bickley*	Fallow	—	,,
	22	Arkengarthdale*	Roe	—	Not numerous
Nottinghamshire	23	Clipstone	Fallow	Numerous	Numerous
	24	Sherwood*	,,	—	Occasional
Lincolnshire	25	Bourne	,,	Not numerous	None observed
	26	Kirby Underwood	,,	,, ,,	,, ,,
Staffordshire	27	Cannock	,,	Numerous	Not numerous
				(Decrease of 75% during war years)	
Shropshire	28	Mortimer	Fallow	Numerous	Numerous
Worcestershire	29	Wyre	,,	,,	Not numerous
Herefordshire	30	Haugh	,,	,,	Occasional
		,,	Roe	(None reported)	Occasional
Northamptonshire	31	Hazelborough	Siberian roe	Not numerous	(None reported)
		,,	Chinese muntjac	(None reported)	Not numerous
	32	Salcey	Siberian roe	Not numerous	Occasional
	33	Fineshade	Fallow	,, ,,	Numerous
	34	Fermyn	,,	Numerous	,,
	35	Yardley	,,	,,	Occasional
		,,	Chinese muntjac	(None reported)	,,
		,,	Siberian roe	Not numerous	(None reported)
	36	Apethorpe*	Fallow	—	Occasional
Rutland	37	Pickworth	Roe	Numerous	(None reported)
Norfolk	38	Thetford	Roe	Numerous	Not numerous
		,,	Fallow	(None reported)	Occasional
Suffolk	39	Brandon	Roe	Numerous	Not numerous
	40	Mildenhall	,,	,,	,, ,,
	41	Kings Forest	,,	,,	,, ,,
	42	Rendlesham	Fallow	Not numerous	(None reported)
Bedfordshire	43	Ampthill	Chinese muntjac	,, ,,	Not numerous
		,,	Siberian roe	,, ,,	,, ,,
Gloucestershire	44	Highmeadow	Fallow	,, ,,	Numerous
Kent	45	Hemsted	Unidentified	,, ,,	(None reported)
	46	Challock	Fallow	Numerous	—
		,,	Japanese	,,	Numerous
	47	Orlestone*	Fallow	—	Occasional
Sussex	48	Goodwood	Roe	Not numerous	Not numerous
		,,	Fallow	,, ,,	,, ,,
	49	Marden	,,	Numerous	,, ,,
		,,	Roe	(None reported)	,, ,,

Table 1 (*continued*)

1	2 Forest		3 Species	4 Density 1938	5 Density 1948
County	No.	Name			
Sussex (*continued*)	50	Slindon*	Roe	—	Not numerous
		,,	Fallow	—	Occasional
	51	Arundel*	,,	—	,,
		,,	Roe	—	Not numerous
Surrey	52	Chiddingfold	Roe	Numerous	Not numerous
Hampshire	53	New Forest	Red	,,	,, ,,
		,,	Roe	,,	,, ,,
		,,	Fallow	,,	Numerous
		,,	Japanese	,,	Not numerous
	54	Ringwood	Roe	Not numerous	Occasional
		,,	Fallow	Occasional	(None reported)
	55	Alice Holt	,,	Not numerous	Occasional
		,,	Roe	(None reported)	,,
	56	Micheldever*	Fallow	—	,,
	57	Alton*	,,	—	,,
	58	Bramshill	Roe	(None reported)	Numerous
		,,	Fallow	Not numerous	(None reported)
	59	Andover*	,,	—	Occasional
	60	Buriton	,,	Not numerous	,,
Wiltshire	61	Gardiner	Roe	,, ,,	,,
		,,	Fallow	(None reported)	,,
(Reported 1938)	62	Westwoods	,,	Not numerous	(None reported)
		,,	Red	(None reported)	Occasional
	63	Savernake*	Fallow	—	Not numerous
	64	Collingbourne*	Roe	—	Occasional
Dorset	65	Puddletown	Roe	Numerous	Not numerous
		,,	Japanese	(None reported)	Occasional
	66	Wareham	,,	Not numerous	Not numerous
		,,	Roe	,, ,,	Occasional
		,,	Fallow	Occasional	(None reported)
	67	Charmouth*	Roe	—	Occasional
	68	Ferndown*	,,	—	,,
Somerset	69	Quantocks	Red	Numerous	Numerous
		,,	Fallow	(None reported)	,,
	70	Bruton	,,	Occasional	Not numerous
		,,	Roe	(None reported)	,, ,,
	71	Brendon	Red	Numerous	,, ,,
		,,	Fallow	(None reported)	,, ,,
	72	Neroche*	Not identified	—	Occasional
Devon	73	Dartmoor	Red	Occasional	Occasional
		,,	Roe	(None reported)	,,
	74	Eggesford	Red	Occasional	Not numerous
	75	Okehampton	,,	,,	,, ,,
	76	Haldon	,,	Not numerous	Occasional
		,,	Fallow	(None reported)	Numerous
	77	Halwill	,,	Not numerous	Occasional
		,,	Red	(None reported)	,,
	78	Lydford	,,	Occasional	(None reported)
Cornwall	79	Bodmin	,,	Not numerous	,, ,,
Anglesey	80	Newborough*	Fallow	-	Occasional
Caernarvon	81	Gwydyr	Roe	Occasional	(None reported)
Merioneth	82	Coed-y-Brenin	Fallow†	,,	,, ,,
	83	Cynwyd	Unidentified	,,	,, ,,
Montgomery	84	Kerry	Fallow	,,	,, ,,
	85	Mathrafal*	,, †	(None reported)	Occasional
Carmarthen	86	Brechfa	Unidentified	Occasional	(None reported)
Glamorgan	87	Cwmogwr*	,,		Occasional
	88	Margam*	Fallow	—	,,
Monmouth	89	Monmouth*	,,	—	Not numerous

† Not positively identified

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THE CAPERCAILLIE IN SCOTLAND

By W. L. TAYLOR, *H.M. Forestry Commission*

(With 1 Figure in the Text)

The capercaillie (*Tetrao urogallus*), sometimes referred to as the Cock of the Forest, and familiarly as the 'caper', has, in Great Britain, long been confined only to parts of Scotland. The species is believed to have occurred in England up to the latter part of the seventeenth century (Witherby, Jourdain, Ticehurst & Tucker, 1941), and earlier to have been widely distributed in the British Islands. The capercaillie is a bird of the pine forests which provide its staple winter food. The progressive destruction of forests in Great Britain since prehistoric times must have been a principal factor in the determination of the final range and fate of the native race of capercaillie. Ritchie records that the bird was regarded as rare in Scotland as early as the sixteenth century, and that some hundred years later numbers were already suffering from the cutting down of conifer forest; in 1621 the Scottish Parliament went so far as to prohibit the buying and selling of 'Caperkayllies', among other species, under penalty of £100 (Ritchie, 1920).

Fig. 1.

It is a matter of ornithological history that capercaillie died, or was killed, out as completely in Scotland in the latter half of the eighteenth century as had previously happened in England and Wales. The species also became extinct in Ireland. The date of its extermination in Scotland is generally accepted as about 1770 (Ritchie, 1920; Witherby *et al.* 1941) (there is, however, a record by Pennant that the 'caper' was still to be met with in Glen Moriston in the year 1769 (Witherby *et al.* 1941)). From this period up to 1837 this handsome game-bird was absent from the British List except for abortive attempts at reintroduction into Scotland in 1827 and 1829 (Witherby *et al.* 1941). Successful reintroductions were, however, made in the vicinity of Taymouth Castle, Perthshire, in 1837 and the following year with birds obtained from Sweden (Ritchie, 1920; Witherby *et al.* 1941). The new stock at once settled down and bred freely. The conspicuous success of the Taymouth experiment was followed by transportations of some of the acclimatized stock and by further importations from Sweden to other parts of Perthshire and Argyll, Ayr and Fife. Meanwhile conditions in several parts of Scotland had become more promising for 'caper'. Since early in the eighteenth century many Scottish landowners had planted extensively with conifers, and subsequent movements of the new stock have, in the main, followed the plantings laid down at this time and afterwards.

Capercaillie have made good use of their opportunities. The spread of the species, up to 1879, is detailed by Harvie-Brown (1879) and, to 1920, by Ritchie. The last-mentioned writer records that 150 'caper' were shot in one day, in 1908, at Blackhall in Kincardineshire—a record for Scotland—and quotes other large bags.

In more recent times local distributions have undoubtedly been affected by the extensive fellings of pine woods which have taken place since 1914, and in some degree already helped by the afforestations and replantings carried out by the State and private owners since 1919. Felling of conifer forest was, of necessity, greatly intensified from 1939 onwards, and the warrantable assumption that the consequent destruction has disturbed many local habitats, and has upset the distribution and density of established capercaillie populations in many districts, has prompted the inquiry into the present status of the species throughout the Forestry Commission's Scottish areas, the result being embodied in the appended table.

The northernmost limit of range in the new forests is at Balblair, to the north-west of Dornoch. This approximates to the northern limit of range shown on Ritchie's map of 1920. Southwards, the species is not reported in any of the Commission's plantations below the Stirling-Perthshire borders. To the west, capercaillie occur in Asknish Forest on the west side of Loch Fyne. In a number of forests, particularly in the neighbourhood of wartime fellings, the bird is said to have decreased in numbers. This is so on the Black Isle, in Glenurquhart, and along the nearby stretch of the Caledonian Canal, also in some of the Aberdeenshire areas, although, in other forests in this county, numbers are tending to increase. In several districts, the felling of adjacent woods has brought in additional birds to the State plantations. At Drummond Hill, close to the *locus* of the successful Taymouth reintroductions of 1837 and 1838, capercaillie are holding their own. The only mention of 'caper' having been adversely affected by the hard winter of 1946–7 comes from the Forest of Deer in Aberdeenshire.

The writer acknowledges his indebtedness to the Commissioners' Director of Forestry for Scotland and the forest officers and foresters in his Directorate, to whose helpful co-operation the material for Table 1 is due.

Table 1. *The distribution of the capercaillie in the Forestry Commission's areas in Scotland,* 1948

County		Forest	Capercaillie	County		Forest	Capercaillie
Sutherland	1.	Dornoch	Not numerous	Aberdeenshire	33.	Alltcailleach	Numerous
	2.	Balblair	Occasional		34.	Auchenriach	Occasional
Ross and	3.	Findon	Not numerous		35.	Bin	Not numerous
Cromarty	4.	Kilcoy	Not numerous		36.	Clashindarroch	Occasional
	5.	Longart	Not numerous		37.	Countesswells	Occasional
	6.	Millbuie	Occasional		38.	Durris	Not numerous
	7.	Morangie	Not numerous		39.	Kirkhill	Not numerous
	8.	Ardross	Not numerous		40.	Midmar	Numerous
Inverness-shire	9.	Craig Phadrig	Occasional		41.	Pitfichie	Occasional
	10.	Craignaneun	Occasional		42.	Tilliefoure	Not numerous
	11.	Culloden	Not numerous		43.	Whitehaugh	Not numerous
	12.	Glengarry	Occasional	Perthshire	44.	Allean	Occasional
	13.	Glenurquhart	Occasional		45.	Blackcraig	Occasional
	14.	Guisachan	Not numerous		46.	Craigvinean	Occasional
	15.	Inchriach	Not numerous		47.	Drummond Hill	Numerous
	16.	Inchnacardoch	Occasional				
	17.	Kessock	Numerous		48.	Keillour	Occasional
	18.	Port Clair	Occasional		49.	Kilfauns	Not numerous
	19.	Queen's (Glenmore)	Numerous		50.	Rannock	Not numerous
					51.	Strathord	Numerous
	20.	Strathdearn	Not numerous		52.	Loch Ard	Not numerous
	21.	Strathnairn	Not numerous	Kincardine	53.	Blackhall	Not numerous
Argyll	22.	Ardgartan	Occasional		54.	Drumtochty	Not numerous
	23.	Asknish	Occasional		55.	Fetteresso	Occasional
Nairn	24.	Ferness	Occasional		56.	Inglismaldie	Occasional
Morayshire	25.	Culbin	Not numerous	Angus	57.	Montreath-mont	Numerous
	26.	Dallas	Not numerous				
	27.	Lossie	Occasional	Fife	58.	Tentsmuir	Occasional
	28.	Monaughty	Not numerous	Stirlingshire	59.	Devilla	Occasional
	29.	Newtyle	Not numerous		60.	Garadhban	Not numerous
	30.	Scootmore	Not numerous				
	31.	Speymouth	Numerous				
	32.	Teindland	Occasional				

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A DISEASE OF MANX SHEARWATERS (*PUFFINUS PUFFINUS*)

By D. SURREY DANE

(With Plate 3 and 2 Figures in the Text)

1. INTRODUCTION

In the autumn of 1946 a severe outbreak of disease occurred among Manx shearwaters (*Puffinus p. puffinus*) on the island of Skomer, Pembrokeshire, in which hundreds of young birds died. A rather similar outbreak followed in 1947, and this was studied in more detail. This paper is chiefly concerned with the 1947 epizootic, though an account of the 1946 epizootic and other relevant information have been included.*

The Manx shearwater is one of the species of seabird which come to Skomer each year to breed. In February and March thousands of shearwaters begin to visit the island after spending the winter at sea. On land they are strictly nocturnal and all visits are made after dark when the danger from gulls and other predators is slight. In May or during the first half of June one egg is laid at the end of a nesting burrow which is often a modified rabbit-burrow deserted by its original owners. Though there are shearwaters nesting in almost every part of the island, the density of population varies greatly. Some of the most crowded colonies are on the slopes above the cliffs and along the walls.

Incubation lasts for a little over 50 days, both birds taking turns to sit on the egg. For a week the young chick is brooded; then it is left alone during the daytime and visited only at night to be fed. When about 60 days old the chick is deserted by its parents who leave the island not to return until the following spring. For the next 10–15 days the young shearwater remains in its burrow unfed, but maturing. Then it makes its way to the sea and like its parents will not visit the island again that year.

At the beginning of its fast the young bird is fat, weighing more than an adult; and its new feathers are hidden beneath a mass of down. By the time it is ready to leave the island it has changed considerably; much of the fat has been used up and only a few traces of down remain.

For the first few nights after desertion the young shearwater stays below ground, then it begins a series of nightly excursions into the outside world. At first these do not take it far from its burrow, but later, as the time approaches for the journey to the sea, it may wander as much as 100 yd. before returning home.

When it is outside at night the young bird takes the opportunity of exercising its wings. If there is a suitable rock or stone nearby it will clamber on to this to do its wing-flapping, and if such perches are scarce several young birds may visit the same one.

For birds reared near the cliffs the journey to the sea is short and they probably leave when a few days younger than their fellows from the colonies in the centre of the island. These birds from the centre of the island may have half a mile of difficult ground over which to run and flap and scramble—for they are not yet able to fly—before reaching the sea.

During 1946 members of the West Wales Field Society were living on Skomer and the shearwater population of the island was under fairly constant observation. For most of the following account of the 1946 outbreak of disease I am indebted to Mr John Buxton, the Hon. Warden of Skomer at the time.

On 31 August 1946 (which is about the time that young shearwaters begin to appear in large numbers), two shearwaters were found in North Valley with blisters on the webs of their feet. Within a week many more birds had been found in the same area some with blistered feet and some with conjunctivitis, these two conditions frequently occurring together. The disease was severe and a large number of birds died. On 22 September 1946, when the last observations were made, shearwaters were still dying, though by then the majority had left the island. In all, many hundreds of young birds died, most of them in North Valley. Two small outbreaks beginning about half way through September were reported from elsewhere; one was in South Valley and the other in the northern part of the island near the Garland Stone (Fig. 1).

Many dead birds were examined and all, with one possible exception, proved to be juveniles.

The conjunctivitis was often severe with a purulent white discharge from the anterior corner of the eyes: it frequently led to blindness before the bird

* Since this paper was written Miles & Stoker (1948) have completed a preliminary investigation of the aetiology of the disease. They find that the aetiological agent is a virus capable of passing through a 'Gradocol' membrane A.P.D. 48 mμ; and they have succeeded in cultivating it on the chorio-allantois of the developing hen's egg.

died. All the sick and dead birds which were found were outside, or just inside their burrows. It is most exceptional to find a normal young shearwater in the open during the daytime, therefore it was concluded that either the sick birds were too weak to return home after a night time excursion, or that the disease produced a desire to sit outside. Several sick birds were kept in captivity, but all died within a few days.

Though no detailed study was made of the disease in 1946 it was clearly most interesting, and plans were made for a further investigation in 1947.

(3) A wall, beside which two birds that had died of the disease were found on the 7th, was chosen for special observation. After dark on the 8th, 9th and 10th, all shearwaters found on or near the wall were ringed. On the 9th, 10th and 11th, recoveries of ringed birds were recorded.

(4) Observations of the habits, behaviour, and condition of young shearwaters were made in both affected and unaffected areas.

(5) Fifteen post-mortem examinations were made on birds which had died of the disease.

Fig. 1. Skomer Island, showing the farm, stone walls and streams. Points A, B and C are referred to in the text.

Skomer was visited at the following times: 24–26 August, 2–4 September, and 7–12 September. On the first visit no sign of the disease could be found, but on the second visit one dead bird which was thought to have died from disease was found. During the last visit an outbreak of disease, in many respects similar to that of 1946, occurred in North Valley, and the following work was undertaken:

(1) On the 8th, 9th and 11th, North Valley was searched for dead and sick birds.

(2) A similar search of most of the remainder of the island was made on the 10th and 11th.

(6) A number of sick birds were kept under observation in captivity.

Unfortunately the epizootic was not studied after 11 September 1947, though at that time there was no indication of it dying down.

2. THE 1947 EPIZOOTIC

During the first and second visits to Skomer, many young birds were examined, but there was no sign of disease until 4 September when a dead juvenile shearwater was found which had probably died on

the previous night. It had lesions which later proved typical of the 1947 epizootic. Fig. 2*a–c* show where and when subsequent cases of dead and dying birds were found in North Valley. The points marked *A*, *B* and *C* in Fig. 1 indicate three other cases of the disease: these were the only ones found outside North Valley. The maps show the rapid spread of the disease from the centre of the island, down North Valley towards the sea.

Out of eighty dead and sick birds which were examined none had conjunctivitis, but all had blisters on the webs of their feet. The blisters varied in size: some were a few mm. across, others covered the whole surface of the web and contained a large amount of fluid. They were found on both the dorsal and plantar surfaces of the feet. In a few cases small yellowish areas were noticed beneath the scales of the tarsus. These were probably similar lesions to those on the webs, but modified by their anatomical position.

A tendency to spastic extension of the legs occurred in a number of sick birds, and it was common to find a dead bird sitting with both legs fully extended. On the day before a bird died it was generally very weak.

The eighty birds examined were all juveniles of about 70 days or more, with the exception of one bird (AT 9378) which was probably between 65 and 70 days old.

The course of the disease was rapid; the birds which were kept under observation in captivity generally died on the third or fourth day after the first appearance of blisters, and no bird survived for more than 11 days. Whether the fatality rate under natural conditions was as high is uncertain, but it is worth mentioning that normal young birds have frequently been kept for about a week in captivity without any ill effects.

Under field conditions the incubation period of the disease may be as long as 8 days, but it may be shorter. Experiments with ducklings, carried out by Miles & Stoker (1948) indicate that for those birds the incubation period is 3–4 days.

The blisters were preceded by a characteristic inflammation of the web. The sequence of events as seen when the web was transilluminated with a torch was as follows: (*a*) Dilatation of the blood vessels of the web. (*b*) Small cloudy areas of oedema appeared in the web. They were pink, presumably because of capillary dilatation, and there were frequently small haemorrhages alongside the visible blood vessels. (*c*) The oedematous areas enlarged and the foot felt appreciably warmer than in a normal bird. (*d*) Blisters developed from the oedematous areas.

The time taken from the first signs of inflammation until the appearance of blisters was about 24 hr. The blisters enlarged rapidly, became yellow and purulent, and then burst. Both feet were not necessarily affected, though this was common. After the first blisters had burst and dried up fresh ones often appeared on other parts of the web. Dilated blood vessels and one or two minor abrasions on the webs of the feet were common in the healthy juvenile shearwaters examined, but the cloudy oedematous areas were characteristic of the disease. Table 1 shows the daily condition of five birds which were under observation throughout the course of the disease.

Table 1. *Course of the disease in five birds first observed before their feet showed signs of inflammation or blisters*

	Days under observation										
Ring no.	1	2	3	4	5	6	7	8	9	10	Time in captivity
AT 9447	N	N	N	N	N	N	I	B	B	B*	Throughout
AT 9454	N	N	N	N	N	N	I	B	B	B*	Throughout
AT 9307	N	N	N	—	B	B	I	B*	—	—	After 2nd day
AT 9481	N	I	—	B	B	B*	—	—	—	—	Last 2 days
AT 9392	N	—	B	B	B	B*	—	—	—	—	Last 2 days

Condition of feet: apparently normal (N); inflamed (I); blistered (B). * Death. No observation (—).

Twenty-eight shearwaters with blistered feet were ringed along the wall (for further details see below). Ten of these were recovered 1, 2 or 3 days later, but none showed any improvement in its condition. Only one of the twenty-eight sick shearwaters was found dead during the daytime. The significance of this will be discussed later.

Judging from the position of sick and dead birds found during the daytime, the morbidity rate was probably highest along the wall where birds were ringed and recovered. It was only here that any attempt was made to estimate the percentage of the population which developed blisters. In all seventy-eight young shearwaters were ringed and examined on or near the wall. Twenty-eight of these as mentioned above had blistered feet. The morbidity rate of 36 % calculated from these figures is probably too low, because a proportion of the younger birds examined might have been expected to develop blisters before they left the island. Better results could have been obtained if the investigations had not ceased on 11 September 1947 when the epizootic was still in progress.

3. TRANSMISSION

Seventy-eight shearwaters were ringed and observations of their habits made along 150 yd. of a wall in September 1947 (see § 1). One of the reasons for doing this was to establish the amount of direct and indirect contact which took place between young birds. From 22.00 hr. until 24.00 hr. the wall and an area 6 yd. on either side of it was searched and all shearwaters found were ringed. Their condition and the time and exact place where they were found was noted. Recoveries of birds ringed on one of the preceding nights were recorded in the same way. Remarkably little disturbance was caused among the shearwaters, which can be picked up and examined very easily.

On either side of the wall for most of its length there was rough grassland thickly overgrown with bracken. The south end was near to the out-buildings of the farm where calves and poultry were kept. A stream ran under the wall at the north end and in this area the bracken was absent. The average height of the wall was about 2 ft., and it was about the same width. It was very old and much of the top was covered by earth, the original stones showing through in places. There were many burrows in the wall and also under cover of the bracken on either side of it.

The following facts relating to contact and movement were observed:

(1) Young shearwaters living in burrows several yards away from the wall came there at night for their wing-flapping exercises. This was understandable because for many of them the wall must have been the nearest place that was suitable and free from bracken. The result was that more birds used the wall than lived in it.

(2) Young birds do occasionally sit touching one another, but this was observed only twice.

(3) There were favourite stones and places on the wall which were used by a number of different birds for their exercises.

(4) A young shearwater when out at night does not necessarily visit one place only for its exercises: it may visit different places many yards apart.

Table 2 gives the movements of all the birds ringed on or within 6 yd. of the wall, and then recovered 1, 2 or 3 days later. Recoveries on the same night often showed that a bird had moved a considerable distance along the wall, but these have been omitted from the table, because handling the birds might have influenced their behaviour.

Though direct contact between young birds was uncommon, opportunities for indirect contact were considerable because many of them walked on the

Table 2. *Movements of juvenile shearwaters ringed on the wall*

Ring no.	Distance (ft.) from south end of wall: 9 July	10 July	11 July	Maximum movement (ft.)	Probable age	Condition of feet
AT 9496	66	38	—	28	< 70 days	Normal
AT 9488	170	144	—	26	,,	,,
AT 9312	144	120	—	24	,,	,,
AT 9393	309	304	303	6	,,	,,
AT 9378	311	312	—	1	,,	Blistered
AT 9364	12	10	—	2	> 70 days	Normal
AT 9365	132	129	—	3	,,	,,
AT 9361	345	339	—	6	,,	,,
AT 9309	—	339	360	21	,,	,,
AT 9377	192	168	—	24	,,	,,
AT 9367	313	—	288	25	,,	,,
AT 9314	99	144	—	45	,,	,,
AT 9457	—	96	152	56	,,	,,
AT 9495	106	—	174	68	,,	,,
AT 9459	—	157	24	133	,,	,,
AT 9320	—	208	39	169	,,	,,
AT 9315	144	438	—	294	,,	,,
AT 9307	—	288	288	—	,,	,,
AT 9392	—	249	240	9	,,	Blistered
AT 9391	—	150	174	24	,,	,,
AT 9399	264	240	226	38	,,	,,
AT 9481	120	—	72	52	,,	,,
AT 9306	—	392	24	368	,,	,,

same ground and used the same stones as one another. It is interesting to note that such indirect contact was probably as high in this particular colony as it was anywhere on the island.

The following points suggest that transmission occurs, or can occur naturally through contact with soil or stones contaminated with blister fluid:

(*a*) Blisters were frequently seen to burst.

(*b*) In the shearwater colony on the wall, opportunity for indirect contact between the feet of young birds was shown to exist.

(*c*) The presence of external lesions only on the feet and tarsus (N.B. the shearwater walks with its tarsus on the ground).

(*d*) There were slight abrasions, which might be necessary for infection to take place, on the feet of most young Shearwaters examined.

Fig. 2*a–c* show the way in which the epizootic spread down North Valley to the sea. A young shearwater from the area of the wall would probably take this route when going to the sea. As some of the birds with blistered feet which were ringed on the wall were still strong and active it is possible that such birds might have spread the disease down North Valley when leaving the island. Most of the dead birds found at the lower end of North Valley were near or in the bed of the stream (which at the time was dried up along much of its course). This is probably explained by the fact that the stream had steep banks on either side and a weak bird moving down the valley would be unable to climb up them.

4. POST-MORTEM EXAMINATIONS

Post-mortem examinations were carried out on fifteen birds which had died of the disease. In eleven cases lung lesions were noticed, but otherwise no definite macroscopic abnormalities were observed except on the tarsi and feet. The lung lesions were small red-brown areas of consolidation, generally one or two were found in any one bird's lungs. In two cases these areas impinged on the ventral surface of the lung and moulds were growing in the abdominal air sacs. A culture from the mould in one of the cases yielded an aspergillas which was kindly identified by Dr G. C. Ainsworth as *Aspergillus fumigatus*. This species has been found growing in the air passages of various birds and of bison in the Zoological Gardens (Rewell & Ainsworth, 1947). Many bacterial contaminants were isolated from culture of blister fluid.

A careful search for ectoparasites was not made, but biting lice were found on the wing feathers of several birds and in two cases mites were found among the body feathers. The mites were kindly identified by Squadron-Leader C. D. Radford as larval forms of *Trombicula autumnalis* (Shaw).

5. NOTES FROM SKOKHOLM

Before the war Lockley (1942) recorded a few isolated cases of disease among Manx shearwaters on the island of Skokholm, which lies just south of Skomer, and is also a breeding ground of shearwaters. He mentions both conjunctivitis and unnatural extension of the legs in some instances.

In August 1947 three juvenile herring-gulls (*Larus argentatus*) died after a few days of sickness. Examination of the corpses revealed that all three had blistered feet, but that none had conjunctivitis.

In September 1947 several hundred young shearwaters were examined for signs of disease. Three were found with the characteristic inflammation of the webs of their feet. All three died after a few days in captivity under observation. Before death they developed conjunctivitis. An apparently healthy bird which may have come into indirect contact with these birds whilst in captivity developed blisters and died.

On 28 September 1947 a juvenile shearwater was found dead with definite blisters on its feet.

The general similarity between the signs of disease mentioned above and those observed on Skomer in 1946 and in 1947 is interesting. It seems likely that there is some intimate connexion.

6. DISCUSSION

The maps showing the time and place where dead and dying birds were found during the daytime probably give a fair picture only of the relative numbers of birds which died in different parts of the island. Many deaths could have occurred within the burrows and passed unnoticed. The fact that only one of the thirty birds with blistered feet ringed on the wall was later found dead suggests that either this happened, or that many sick birds were strong enough to make the journey to the sea.

The uniformity in the age of affected birds (see above) was most striking, and probably means that infection took place soon after they began their nightly excursions. Any later infection might have failed to produce blisters before the young bird left the island, in which case the disease could not have spread. The slightly longer time which the birds from the centre of the island spent before leaving for the sea would therefore have favoured the spread of the disease among them. On the other hand, if young birds living above the cliffs became infected they would stand a good chance of leaving before the incubation period of the disease was over.

Though an explanation has been offered to account for the spread of the disease among a population of young shearwaters, so far there is no indication of the manner in which an outbreak originates. There is

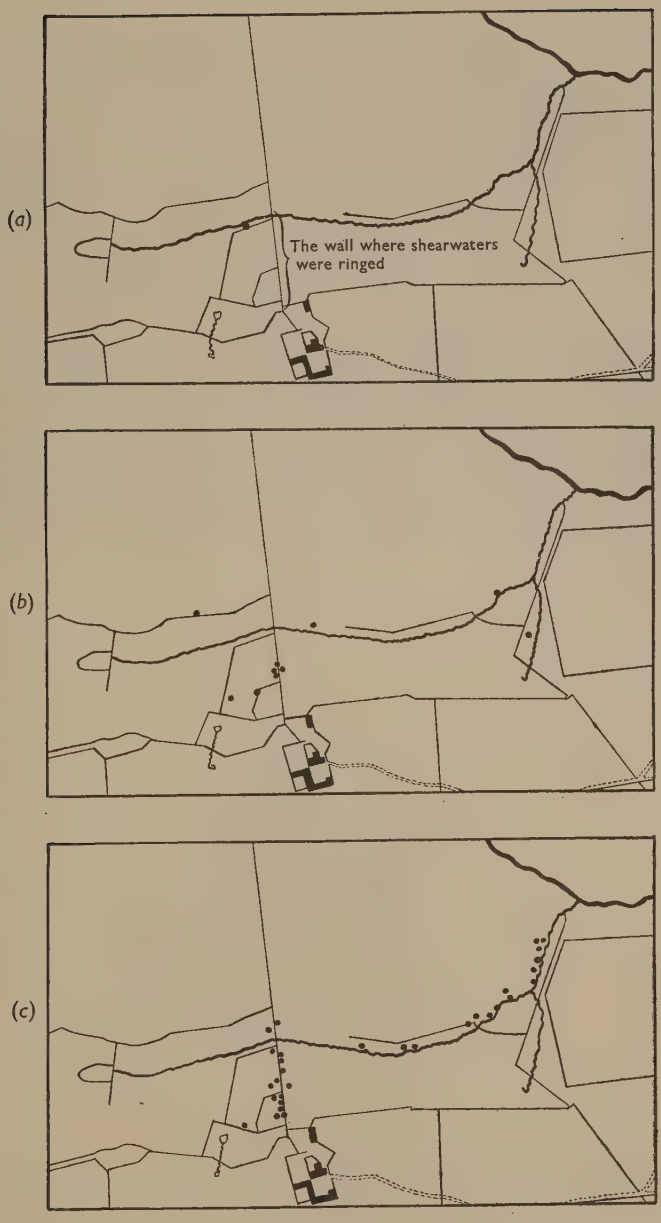

Fig. 2. North Valley. Dots show where dead or dying shearwaters were found: (*a*) 4 July, (*b*) 5–8 July, (*c*) 9–11 July 1947.

some evidence that sporadic cases apparently unconnected with epizootics have occurred both on Skomer and Skokholm. It is possible that each year there are a number of these sporadic cases in different parts of both islands, but that epizootics can only arise from them in certain rather exceptional circumstances. The nature of the colony where a sporadic case occurs, its situation, its density of population, and the habits of its inmates may well be the factors which determine the extent to which the disease will spread.

How the sporadic cases become infected is not known. At the moment, what knowledge we have of the disease is largely confined to its epizootic form.

7. SUMMARY

1. An epizootic among Manx shearwaters (*Puffinus p. puffinus*) was observed on Skomer island in September 1947. It had many features in common with an epizootic observed there in the autumn of 1946; the chief point of difference between the epizootics being the absence of any cases of conjunctivitis in 1947.

2. The signs of the disease were found in juvenile shearwaters, generally between 70 and 75 days old.

3. The principal lesions of the disease were blisters on the webs of the feet and small areas of consolidation in the lungs.

4. Fatality was probably high; the morbidity rate varied with the locality.

5. Evidence was obtained that the incubation period of the disease was about 8 days or less, and that the most likely mode of transmission was by contact of the webbed foot with soil or stones contaminated from burst blisters.

6. The manner in which an epizootic arises is obscure, and it is possible that other hosts exist besides the shearwater.

8. ACKNOWLEDGEMENTS

I am most grateful to Prof. E. T. C. Spooner for his valuable help and advice, both on Skomer and in the preparation of this paper. The observations on Skokholm were kindly made by Mr John Buxton, Mr Peter Conder and Miss J. Keighley.

I would like to thank Mr and Mrs Codd who gave permission for this work to be carried out on Skomer.

The description of the habits of the Manx shearwater given in the introduction is based on the work of Mr R. M. Lockley, whose study of this species was referred to constantly during the investigation of the epizootic.

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Photo J. Fursdon

Photo 1. Juvenile Manx shearwater ready to go to sea.

Photo J. Fursdon

Photo 2. Blister on the web of the foot of a sick juvenile shearwater (approx. natural size).

THE LETHAL TEMPERATURES OF SOME COMMON BRITISH LITTORAL MOLLUSCS

By RONALD GEORGE EVANS, *formerly University College of Wales, Aberystwyth*

(With 2 Figures in the Text)

1. INTRODUCTION

The zonation of the more common British littoral molluscs is known from the work of various shore ecologists, but the causal factors which determine the vertical limits of distribution of these species between tide-marks are largely a matter of conjecture. Among what might be considered as the local climatic factors acting on intertidal organisms exposed to the air it appears that temperature, desiccation and possibly light effects are the most critical, i.e. the 'heat-light-desiccation' complex. In the case of organisms which inhabit permanent rock pools, the desiccation factor is eliminated, and it is likely that changes in the temperature and salinity of these pools during periods of exposure will be important. Intertidal algae have been the chief subject of investigations along these lines, and relatively few studies have been made on littoral fauna. The effect of heat, desiccation and salinity on a series of six gastropods has been studied experimentally by Broekhuysen (1940) in False Bay, South Africa, while Gowenloch & Hayes (1926) have investigated the action of certain factors of the physical environment on three species of *Littorina* in Canada. Little work of a similar nature seems to have been done on the British littoral molluscs, even though experimental work of this type could be used with advantage to supplement the data obtained in the field by shore ecologists.

From what is already known it appears probable that the effects of temperature acting as an isolated factor (i.e. 'pure temperature effects') are of subsidiary importance to the drying action of supernormal temperatures in controlling the upper limits of distribution of littoral plants and animals. Thus in the case of the South African molluscs it was found that between the temperatures necessary to kill the snails in the laboratory and the temperatures to which they are normally subjected in their natural environment, there exists a sufficiently wide difference to rule out the possibility of heat death among these species on the shore. This principle will be examined with respect to certain British molluscs.

Huntsman & Sparkes (1924) demonstrated that for marine organisms in general the degree of resistance to heat is correlated with the temperature ranges at which such species exist in nature. Gowenloch & Hayes (1926) reported that individuals of the same species (*Littorina littorea*, *L. rudis* or *L. palliata*) collected from different tidal levels on the shore exhibit a gradation in thermal death temperatures, i.e. a 'tidal level differentiation' exists in lethal temperatures. Henderson (1929) has shown that, among the lamellibranchs, deep-water forms are less tolerant of heat than those occurring in the lower part of the intertidal zone, that these in turn are less tolerant than upper-shore species, while lamellibranchs characteristically found in warmer waters are the most tolerant of all. Finally, Broekhuysen (1940) found that the series of thermal death points for his six gastropods is identical with the order in which these species are zoned on the shore of False Bay, *L. knysnaensis*, occurring to well above extreme high water of spring tides, has a lethal temperature of 48·6° C.; *Oxystele sinensis*, which barely reaches mean sea level, dies at 39·6°; while the other four are zoned between these two species and have thermal death points intermediate between these temperatures. He also showed that, in their ability to withstand prolonged high temperatures, the six snails fall into a similar series. Furthermore Broekhuysen tabulates the lethal temperatures of a series of marine molluscs as determined by Vernon (1899), Gowenloch (1926), Gowenloch & Hayes (1926) and Henderson (1929), and concludes that 'generally speaking, the lowest lethal temperatures are found in snails inhabiting the lowest levels, while lethal temperatures increase with increasing height above low water level'. Thus, from all the evidence, it would appear that there exists a fairly definite correlation between the ability of various snails to withstand pure temperature effects and the temperatures to which they are likely to be exposed in nature.

In the present paper, the results of experiments on eleven molluscs common on the shores of Cardigan Bay are described. The following species were chosen: *Littorina neritoides* (L.), *L. rudis* (Maton), *L. littoralis* (L.), *L. littorea* (L.), *Gibbula cineraria* (L.), *G. umbilicalis* (da Costa), *Patella vulgata* L., *P. depressa* Pennant, *P. athletica* Bean, *Nucella lapillus* (L.), *Osilinus lineatus* (da Costa).

The distribution and zonation of these in Cardigan

Bay have been described previously (Evans, 1947*a*, *b*). The purpose of the work is twofold: first, to obtain some idea of the thermal death points of the molluscs for comparison with temperatures which they experience on the shore, in order to investigate the possibility of heat death among these forms in nature; secondly, to determine whether there is any correlation between the heat resistance of such species and their vertical zonation. In order to investigate the effect of temperature acting as a single factor, it is necessary to eliminate the desiccation effect. Thus all the experiments were performed on submerged snails; the ability of the molluscs to withstand both desiccation and salinity presents a separate problem, at present under investigation. The present results are divided into three sections. The first part deals with the thermal death points, the second with the ability of the snails to survive under conditions of prolonged exposure to supernormal temperatures, and this is followed by a general discussion of the results. Any discussion of the actual mechanism and causes of heat death does not fall within the scope of this paper, but it should be noticed that Heilbrunn (1943) gives a concise summary and an extensive list of references dealing with this aspect. The paper by Heilbrunn, Harris, Le Fevre, Wilson & Woodward (1946) on the toxic factor which is introduced during heat death describes recent advances in this field.

2. THE THERMAL DEATH POINTS OF THE MOLLUSCS

Heilbrunn (1943, p. 420) has pointed out that there are very few useful records of heat-death temperatures, since the time factor (i.e. the rate of heating) is so often neglected. It is known that the rate at which a species is heated will affect its ultimate death point; thus Rees (1940) found that the flatworm *Monocelis fusca* dies at 37° when heated up as slowly as 1° per day, but that when the rate is increased to 1°/30 min. the animal survives to 44°. It would appear that the duration of exposure to each step in a gradually increasing temperature scale will affect the final death point; therefore, it is important to settle on some standard rate. Not all workers on thermal death points have paid attention to this factor or have given detailed descriptions of their methods, but Gowenloch & Hayes (1926) and Broekhuysen (1940) adopted a standard temperature increment of 1°/5 min., assuming that this is sufficiently slow to make any lag between the body temperature and that of the surrounding water small enough to be neglected. This same standard rate has been adopted in the present experiments so that the results may be compared with theirs. In the case of the three species of limpets additional experiments, based on a scale of 1°/15 min., have been carried out. Therefore some indication is obtained of the variations in lethal temperatures which might be expected when the rate of heating is slowed down.

Preliminary experiments seemed to indicate, for the limpets at least, that the thermal death points may also vary according to the time of the year. Limpets collected from the shore during the very cold early months of 1947 were found to be less tolerant of heat than those collected and used for experiment in June and July. In order to obviate any such possible differences, all the experiments were performed during the summer months (June–September) of 1947; moreover all the test animals were kept overnight in a glass aquarium of aerated sea water at room temperature before experiment.

The method of procedure was similar for all the species. A number (depending on the size of the test animals) was placed in a 500 ml. beaker of sea water of 20°, suspended in a larger vessel (1 l.) of tap water, and the whole apparatus was gently heated by a gas burner. With care and attention it was possible to adjust the rate of heating to the scale adopted with a good degree of accuracy. During the heating process notes were continually made on the behaviour of the test animals in comparison with the behaviour of individuals maintained at 20° as a control. Tests of the salinity showed that only a very slight and negligible increase is observed during the 2½ hr. necessary to raise the temperature from 20 to 50° at a rate of 1°/5 min. When the rate was slowed to 1°/15 min. suitable quantities of glass-distilled water, first heated to the correct temperature, were added every 2 hr. During the shorter experiments aeration was effected by rigorous stirring; during the longer ones a simple aerating apparatus was used.

At temperatures just above 30° most species showed some signs of distress; active crawling usually ceases and a little later even the slight movements of the tentacles and foot also cease. After this the animals were tested (without removing them from the water) for irritability by pricking with a needle. When they no longer displayed any sort of response, i.e. when 'heat coma' set in, five or ten of the animals were removed at suitable intervals. During the preliminary experiments, test animals were removed at intervals of 2°, in subsequent experiments at intervals of 0·5°. These were placed in beakers or dishes of sea water of the same temperature as the water from which they were removed. After cooling for 1 hr. they were re-examined for signs of life. Those which responded to stimulation were considered to have recovered from heat coma; those displaying no response were considered dead, and the lethal temperature was taken as the minimum temperature at which at least 50% of the snails failed to recover. When the snail died in a retracted condition, the shell was broken in order to facilitate the final examination. For each

species, a preliminary experiment first indicated the rough limits, and at least three subsequent experiments were performed, removing test animals at temperatures between these limits. The preliminary experiments are not included in the results. By removing at least five (seven or ten of the smaller species) at each interval individual variation tends to be equated, and by repeating each experiment several times any variations in the conduct of the observer are checked. The final figure is taken as the mean of all the experiments excluding the preliminary ones.

Patella. All three species of limpet, *P. vulgata*, *P. depressa* and *P. athletica*, behave similarly during the heating process. At first they are quite active, waving their tentacles and straining out of their shells (they were all placed foot uppermost in the beaker to facilitate observation). This active movement slows down rapidly when 26° is reached, and from 30 to 32° very little spontaneous movement occurs. All respond to stimulation until the temperature reaches 37–38°; after this the limpets pass into a comatose state and the edge of the mantle often tends to curl away from the shell. If they are removed at 38° and allowed to cool the animals recover fairly quickly, but at higher temperatures recovery takes longer and is less complete. Finally, at the thermal death point, no recovery occurs even after cooling for an hour. Table 1 gives the results for the three species, both on a 1°/5 min. scale and one of 1°/15 min., and for experiments performed in February–March and in June–July. It will be noticed that the heat-death temperatures are higher in the summer months than in the winter, and that slowing down the rate of heating from 1°/5 min. to 1°/15 min. results in a noticeable lowering of the lethal temperatures.

Table 1. *Lethal temperatures of species of* Patella *at different seasons*

Time of year	Rate of heating	*P. vulgata* Results (° C.)	*P. vulgata* Mean (° C.)	*P. depressa* Results (° C.)	*P. depressa* Mean (° C.)	*P. athletica* Results (° C.)	*P. athletica* Mean (° C.)
June–July	1°/5 min.	42·5, 43, 43	42·8	43, 43·5, 43·5, 43	43·3	42, 41·5, 41·5	41·7
	1°/15 min.	42, 42, 42	42·0	42·5, 42·5, 43, 42·5	42·6	41, 41, 40·5, 41·5	41·0
Feb.–Mar.	1°/15 min.	40·5, 40, 40·5	40·3	41, 41, 41	41·0	39·5, 39, 39·5	39·3

The results quoted in Table 1 were obtained with limpets collected from tide pools on the upper shore. Other experiments were conducted on individuals from other habitats, e.g. from low-tide pools, from sun-baked rocks at various tidal levels, from shaded overhangs and from under weed. No significant differences, correlated either with tidal level or with type of habitat, could be detected.

Littorina littorea. Normal activity continues during heating up to about 32°, the snails attempting to scale the sides of the beaker under the stimulus of negative geotropism. After this activity has ceased irritability is still retained as high as 39°. Three separate experiments gave results of 46° as the thermal death point of the species. *L. littorea* is one of the species for which Gowenloch & Hayes (1926) demonstrated 'tidal level differentiation' in the lethal temperature. At St Andrews, New Brunswick, these workers found that 'low-tide' snails died at 41 +°, 'mid-tide' snails at 43·5°, and 'high-tide' individuals at 43·7°. During the present investigation no significant differences in the temperature of heat death could be detected between *L. littorea* collected (*a*) from the high-water neaps region, and (*b*) from between low-water neaps and springs. It should be noticed that 46° is considerably higher than the St Andrews figures quoted above, but, working at Halifax, Nova Scotia, later in the year, Gowenloch & Hayes (1926) obtained a thermal death point of 46·6° for this species. This they ascribe to the fact that the sea temperature at Halifax is a few degrees higher than that at St Andrews, suggesting that the littoral fauna at the former locality is naturally adapted to somewhat higher temperatures than it is at St Andrews. At all events, the Halifax results are more in accord with the writer's experiments.

Littorina littoralis. Two series of experiments were performed: (*a*) with snails from the *Fucus spiralis* zone (around mean high-water neaps), and (*b*) with snails from the lower end of the *Ascophyllum nodosum* zone (below low-water neaps). The following results were obtained:

group (*a*)	45°	44°	44·5°
group (*b*)	44°	44·5°	44·5°

i.e. there is no significant difference between the two groups, and the mean of the six determinations is approximately 44·3°.

Like *Littorina littorea*, *L. littoralis* continues to be active up to 32°; but slight movements of the foot and tentacles can be detected up to 34°, and the species passes into a comatose condition, losing all irritability, at 36°, i.e. at a slightly lower temperature than does *L. littorea*.

Littorina rudis. Again, two sets of individuals were experimented with: (*a*) from high-water neaps,

and (*b*) from 3 ft. above mean high-water springs. The results were:

group (*a*)	44·5°	45°	45·5°
group (*b*)	45°	45°	45°

i.e. no significant differences occur and the mean for the lethal temperature is 45°. Gowenloch & Hayes (1926), at St Andrews, quote results of 42·4° for 'low-tide' individuals, 43° for 'mid-tide' snails, and 43·2° for 'high-tide' individuals, all of which are appreciably lower than the present results.

Active crawling in *L. rudis* appears to be possible at temperatures up to 32°, slight movements can be detected to about 35°, irritability finally ceases at 37°.

Littorina neritoides. All the snails used were collected from between mean and extreme high-water springs. The species crawls very readily up the sides of the beaker until the temperature reaches the neighbourhood of 30–31°. All movement ceases at 34°, and coma sets in at 38°. In three separate experiments, death occurred at 46, 46·5 and 46·5° respectively, giving a mean thermal death point of 46·3° for *L. neritoides*.

Gibbula umbilicalis. Material was collected from the mid-tide level of the shore only. This species also tends to crawl up the sides of the vessel until the temperature reaches 26–27°. Above this, although active crawling continues to about 31°, it appears to be purposeless and with no definite direction, as if the snails' sense of geotropism is somehow impaired. No spontaneous movement of any kind can be detected above 33°, irritability is lost at the same time, and a state of coma intervenes almost immediately, i.e. between 33 and 34°. The temperature of heat death was given by five separate experiments as 41, 43, 42, 42 and 42·5°, with a mean value of 42·1°.

Gibbula cineraria. This species is not very common in Cardigan Bay, and owing to the difficulty of collecting sufficient material, batches of three individuals, instead of five, were removed at each temperature increase. All were taken from levels below mean low-water springs. The snail crawls actively up to temperatures of 26–27°; above this, slight tentacle movements can be detected up to 30–31°. Coma sets in at about 34°, and death occurred in three separate experiments at 36, 36·5 and 36°, giving a mean of 36·2°.

Osilinus lineatus. Crawling continues up to 33°, but while at first the direction of progression is vertical, above 31° negative geotropy seems to be lost and the crawling is random. Slight movements occur until 37° is reached, coma intervenes shortly after (38–39°), and the thermal death point was given as 46, 46, 45·5 and 46° by four separate experiments, i.e. a mean of 45·8°. All the specimens were taken from just above mean tide level on the shore.

Nucella lapillus. Snails were collected from levels between high and low water of neap tides. Even in sea water at room temperature *Nucella* is extremely sluggish, and if touched it withdraws into its shell and does not re-emerge for some time. Thus it is impossible to state at what temperature crawling ceases, since the snails are not at all active during any part of the experiment. Irritability seems to be lost and coma sets in at 37°, and 40° was obtained as the lethal temperature in three separate experiments.

Table 2. *Lethal temperatures of all the species studied (summer season).*

Rate of heating 1°/5 min.

Species	Temp. (° C.) at which spontaneous movement ceases	Temp. (° C.) at which irritability is lost (heat coma)	Temp. (° C.) of thermal death (mean values)
Littorina neritoides	34	38	46·3
L. littorea	32	39	46·0
Osilinus lineatus	37	38–39	45·8
Littorina rudis	35	37	45·0
L. littoralis	33–34	36	44·3
Patella depressa	31–32	37–38	43·3
P. vulgata	31–32	37	42·8
Gibbula umbilicalis	33	33–34	42·1
Patella athletica	30–32	37	41·7
Nucella lapillus	?	37	40·0
Gibbula cineraria	30–31	34–35	36·2

Table 2 summarizes the above results. The species are arranged in order of decreasing death temperatures, and the temperatures at which normal activity ceases and those at which heat coma intervenes are also figured. It will be observed that there is no relationship between these three series of temperatures, which is what Broekhuysen (1940) also concluded in the case of the six South African molluscs (1940, Table 4 and p. 272). This worker did find, however, that the sequence of lethal temperatures for these snails was identical with their order of vertical

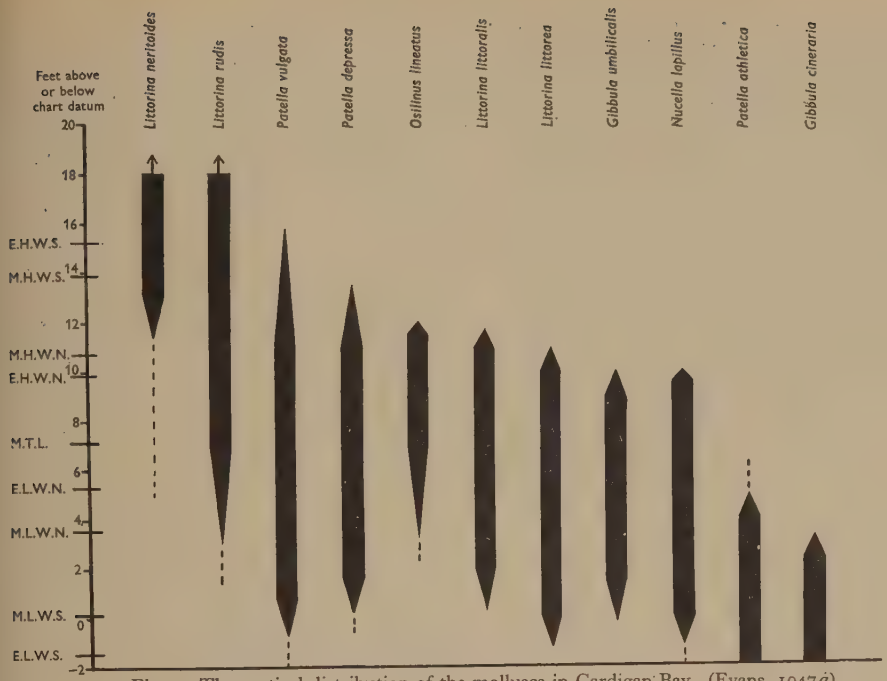

Fig. 1. The vertical distribution of the molluscs in Cardigan Bay. (Evans, 1947*a*).

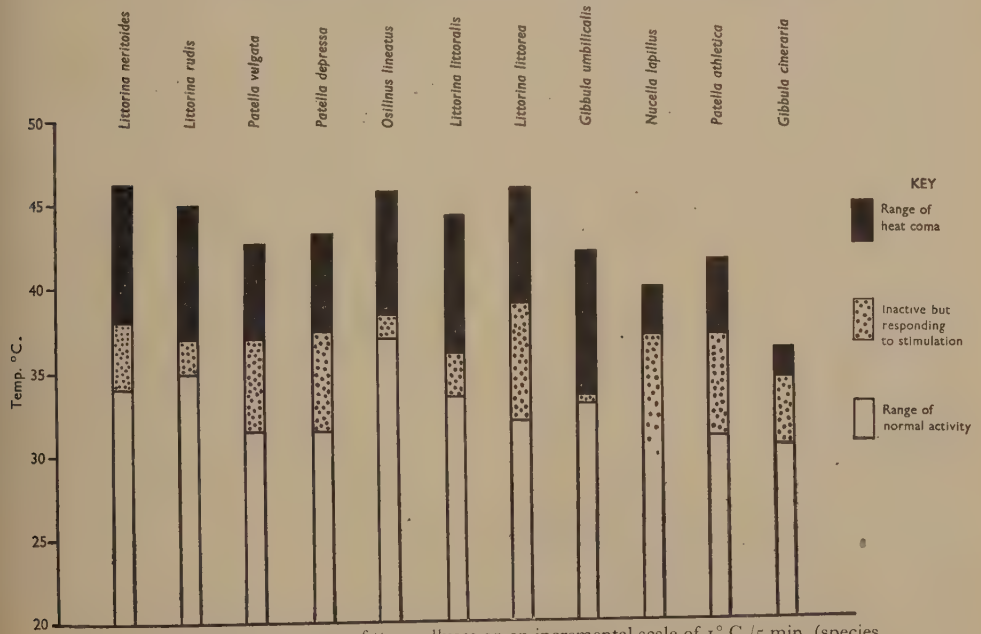

Fig. 2. Temperature ranges of the molluscs on an incremental scale of 1° C./5 min. (species arranged in order of vertical zonation, see Fig. 1).

zonation in False Bay (1940, figs. 5 and 1). A similar relationship does not appear to be true for the British molluscs. In Fig. 1 I have summarized my findings (Evans, 1947*a*, *b*) with regard to the zonation of the eleven species, while Fig. 2 gives the thermal death points, temperature of heat coma, etc., of the molluscs arranged in the same order as in Fig. 1. It is immediately apparent that no correlation exists. *Littorina littorea* and *Osilinus*, for example, are much more tolerant of increasing temperature than either *Littorina littoralis*, *Gibbula umbilicalis* or *Nucella*, yet all five species have their upper limits of zonation in the high-water neaps region. It is true that *Gibbula cineraria*, which only occurs at very low levels, has the lowest thermal death point, and that *Littorina neritoides*, occurring to well above high-water springs, has the highest; but apart from this there is very little obvious correlation between the order of vertical zonation and the series of either the thermal death points, the temperatures of heat coma, or the temperatures at which active movement is impaired.

Table 3. *Comparison of the lethal temperatures of South African and British molluscs, and percentage exposure to the air experienced by the species*

Species	% exposure limits	Lethal temp. (° C.)
South African spp. (Broekhuysen, 1940)		
Littorina knysnaënsis	10–100	48·6
Thais dubia	−5–100	41·7
Oxystele variegata	−5–100	42·1
O. tigrina	10– 95	40·5
Cominella cincta	0– 90	39·5
Oxystele sinensis	0– 45	39·6
British spp. (Evans, 1947*a*)		
Littorina neritoides	20–100	46·3
L. rudis	8–100	45·0
Patella vulgata	0–100	42·8
P. depressa	0– 92	43·3
Osilinus lineatus	22– 82	45·8
Littorina littoralis	4– 81	44·3
L. littorea	7– 71	46·0
Gibbula umbilicalis	2– 63	42·1
Nucella lapillus	0– 62	40·0
Patella athletica	0– 42	41·7
Gibbula cineraria	0– 21	36·2

In Table 3 a comparison is made of the British and South African molluscs. Broekhuysen (1940, Table 3) gives figures for the percentage exposure to the air of the various shore levels between which his six gastropods are zoned; similar figures for Cardigan Bay have been estimated previously (Evans, 1947*a*, Table 3). Here again there is little similarity and it seems that there is no direct correlation between heat-death temperatures and the percentage exposure to the air experienced by the various species.

The thermal death points of the eleven species are high in comparison with the normal temperatures experienced in their environment, except possibly in the case of *Gibbula cineraria*. This snail is, however, confined to low levels on the shore, and even when these levels are uncovered the mollusc is normally to be found only in pools, under stones or in patches of weed, i.e. in damp, shaded situations. Under such conditions it is unlikely that *G. cineraria* is ever exposed to temperatures much higher than that of the sea. Altogether then it is improbable that, in the case of individuals of any of the species when they occur in tide pools, the snails are ever subjected to temperatures approaching the thermal death point. In order to confirm this, recordings were made on the shore during the summer months of 1947, and these were supplemented from past records. The highest temperature found in rock pools never exceeded 30°, even on days when the maximum shade temperature of the air was as high as 27°, and when sun temperatures of almost 40° were recorded. Thus those snails inhabiting pools never experience temperatures comparable with those necessary to kill them.

Species such as the limpets, the periwinkles (especially *Littorina littorea*) and *Osilinus lineatus* are, however, commonly found sitting on rocks and stones which are fully exposed, sometimes for hours, to the hot sun. In attempting to measure the temperatures experienced by such animals several difficulties emerge. When the snails are immersed in water it is probable that they achieve the temperature of their immediate environment fairly rapidly, but when they are exposed to the air no such assumption is permissible. Factors such as the temperature of the substratum, the radiation of heat from the shell and from the rock surface, the ability of the shell to absorb heat from the air and from the rock, and the transmission of heat from the shell and rock to the soft inside tissues of the animal are all important. Air temperatures at the surface on sun-baked rocks and boulders were recorded and the highest reading obtained was 40·5°, but it does not follow that animals situated on such rocks ever experienced such high temperatures. Attempts were made to measure body temperatures of limpets by removing the animal from the surface and immediately plunging an ordinary mercury thermometer into their soft tissues, but the highest recordings obtained by this highly unsatisfactory method never exceeded 26°. Furthermore, specimens removed from hot rocks and examined immediately usually withdraw into their shells or display some other active movement; comparing their condition with their behaviour under experiment it seemed clear that in their natural environment the body temperature they attain is below that which is

necessary to induce either heat coma or a suspension of the faculty of spontaneous movement. Finally, no indication of heat death in nature among the population could be observed during the very hot summer of 1947. Therefore it seems fairly well established that the molluscs studied never experience, on the shore, temperatures approaching those which prove lethal to them in the laboratory.

3. THE RESISTANCE OF THE MOLLUSCS (WHEN SUBMERGED) TO PROLONGED HIGH TEMPERATURES

The survival times of all the species, continuously submerged in normal sea water at 40°, have been determined. Experiments at 35° have been performed on five of the species, i.e. *Patella vulgata*, *Gibbula umbilicalis*, *Patella athletica*, *Nucella lapillus* and *Gibbula cineraria*, and the survival times of the last two at 30–31° have also been determined.

The method of experiment was as follows: An electrically heated oven with adjustable thermostatic control was regulated to maintain a glass trough of sea water contained within it at the requisite temperature (30, 35 or 40°). A number, between 30 and 50, depending on the size of the individuals, of the species under investigation was immersed in a beaker of sea water at 20°, and brought to the temperature of the oven at a steady rate of 2°/5 min. They were then immediately transferred to the trough in the oven, the time being noted. At intervals five animals were removed, together with some of the heated water, and left to cool in Petri dishes for the space of 1 hr. After this they were examined, as previously described, for signs of life. For each species three separate experiments were conducted. During the first of these, batches were removed at hourly intervals in order to determine the rough limits of survival. Subsequent experiments involved the removal of batches at intervals of 15 or 30 min. between these limits. Aeration was effected by means of a simple aerating apparatus, the delivery tube of which led through one of the airvents of the oven and into the trough. Salinity was controlled by the periodical addition of measured volumes of glass-distilled water, first heated to the temperature of the oven.

The results are summarized in Table 4. It is evident that, with the exception of *Osilinus lineatus*, the survival times fall into a sequence identical with that of the thermal death points, but not of the order of vertical zonation.

Temperatures of 40° (i.e. 104° F.) are very rarely experienced on the shore, and even when rocks are fully exposed to the sun on hot summer afternoons such high temperatures are never prolonged for many hours. Furthermore, although the rock surface may reach 40°, it has already been pointed out that this is no indication that the snails' body temperatures ever reach this level; indeed, the evidence suggests that the molluscs never experience temperatures even high enough to inhibit spontaneous movement or to produce heat coma. Even if they did heat up to 40°, the experimental evidence indicates that the four species of *Littorina*, together with *Patella vulgata*, *P. depressa* and *Osilinus lineatus* can withstand such temperatures (when the danger of desiccation is eliminated) for several hours. *Patella vulgata* and *Gibbula umbilicalis* can exist for over 10 hr. at 35°, *Patella athletica* for over 8 hr., *Nucella* for almost 3 hr. and *Gibbula cineraria* for over 1 hr. Finally, *Nucella* survives at 30° for over 8 hr., which is longer than it ever remains uncovered by the tide, and *Gibbula cineraria*, which is never exposed for more than 2 hr., can withstand a temperature of 30° for 5 hr.

Table 4. *Survival times of the species studied, on prolonged exposure to supernormal temperatures*

Species	Temp. (° C.)	Survival time (hr.)
Littorina neritoides	40	14–15
L. littorea	40	11·5–12
Osilinus lineatus	40	6–6·25
Littorina rudis	40	9·5–10
L. littoralis	40	4·25–4·5
Patella depressa	40	3·5–3·75
P. vulgata	40	2·75–3
	35	10
Gibbula umbilicalis	40	0·75–1
	35	10
Patella athletica	40	0·75–1
	35	8·5–9
Nucella lapillus	40	0–0·25
	35	2·5–3
	30	8
Gibbula cineraria	40	0
	35	1·25–1·5
	31	5–5·25

4. DISCUSSION

From the experiments it can be concluded that all the molluscs are temporarily tolerant of higher temperatures than they are likely to experience on the shore, and that they can also survive at supernormal temperatures for longer periods than they are ever called upon to withstand in nature. The possibility of heat death amongst these species in their natural environment appears to be very remote, and pure temperature effects do not seem to be of much importance as causal factors determining the upper limit of distribution of these forms between tide marks. This is not only a confirmation of Broekhuysen's (1940) conclusions and in agreement with the opinions of several other authorities, but also a confirmation of what may be observed in the field. Even during what

must be considered as the abnormally hot summer of 1947 the writer was able to find no evidence of thermal death amongst these snails on the shores of Cardigan Bay.

Although temperature effects seem to be of little importance in controlling the zonation of the molluscs on open rock, there remains the possibility of temperature being a causal factor in the zonation of these species in tide pools. Again, however, there is no evidence of this. Although *Osilinus* and *Littorina littorea*, for example, both display a high degree of heat-tolerance, neither species is to be found in the highest of rock pools; yet *Littorina rudis*, *Patella vulgata*, *P. depressa* and *P. athletica*, all of which have lower thermal death points than *Osilinus* and *Littorina littorea*, are common in pools well above high-water springs. There are two possible explanations for this. First, it may be that neither of these two species is capable of withstanding the high salinities experienced in the highest pools during long periods of dry weather; this possibility will be dealt with in a subsequent investigation. Secondly, as Stephenson (1941) remarks, 'animals and plants may find their *optimum* conditions at temperatures and salinities well below their actual lethal limits', and we have no basis for the assumption that the lethal temperature is in any degree an indication of the level of the optimum. It is not impossible that, although the lethal limits of temperature for *Osilinus* and *Littorina littorea* are higher than those for *L. rudis* and the limpets, their optimum conditions of temperature may be actually lower.

The thermal resistance of the eleven species, measured either by their lethal temperatures or by their survival times at supernormal temperatures, does not follow their zonational sequence on the shore as Broekhuysen (1940) found to be the case for the six South African gastropods. Thus, comparing Figs. 1 and 2, *Osilinus lineatus*, *Littorina littorea* and *Patella athletica* appear to have higher thermal death points than their vertical zonation would warrant, while *Patella vulgata*, *P. depressa* and *Nucella lapillus* have rather low lethal temperatures. At first sight this would seem to contradict the principle that the heat resistance of a species is correlated with the temperature range which is normal in its environment, since, generally speaking, the higher one proceeds up the shore from low water the more exposed is the environment to high temperatures. This, however, is only a generalization. On an irregular rocky beach, such as occurs in the centre of Cardigan Bay, we can distinguish between two types of habitat: (*a*) the south and south-western faces of rocks and boulders, receiving the maximum amount of illumination and heat, and (*b*) the north and north-eastern faces of peaks and ledges, overhangs, etc., which may be almost perpetually shaded from the heating effect of the sun. Both *Osilinus* and *Littorina littorea* are commonly found in the first type of locality. Even at mean high-water neaps (i.e. at the upper limit of their distribution) these snails occur in appreciable numbers on smooth rocks and boulder faces, where temperatures of 40° have been recorded (see p. 170). Again, *Patella athletica*, though it appears on open rock only on the lower beach, occurs in rock pools up to above mean high-water springs. Comparing this with *Gibbula cineraria*, which is never present, even in pools, above mean low-water neaps, it is not surprising that the limpet is found to have an appreciably greater degree of heat resistance. The relatively high thermal death points of these three species are thus correlated with habitat characteristics independent of tide level.

Both Orton (1929) and the writer (Evans, 1947*b*) have commented on the restriction of *Patella vulgata* to shady and damp situations at levels above mean high-water neaps. Even in the high-water neaps region, the limpet is not as common as *Osilinus*, for example, on sun-baked boulders, and its lower degree of heat-resistance may be correlated with this. *Nucella lapillus* is even more restricted to shade near its upper limit, and I have previously stated (1947*a*) that 'the greatest numbers are to be found on steep but sheltered landward or north-eastern faces of reefs, rock masses or large boulders', suggesting that 'shade may play some part in the choice of such a habitat, especially at high levels'. The maximum shade temperature at Aberystwyth (Harbour Master's records) rarely exceeds 25°, and the mean for the summer months is in the region of 20°. Actual recordings I have made in *Nucella* habitats confirm the fact that the snail is rarely, if ever, called upon to withstand temperatures above 25°, even on the assumption that it heats up to the temperature of the surrounding air, which is doubtful. With regard to *Patella depressa*, although this limpet is frequent on rock faces exposed to the south and west, these rocks are generally peaks which rise from the shore on the lower part of the beach, and are invariably exposed to a great deal of surf. Splash and spray are thrown up on such peaks on most days, and for a considerable part of the tidal period. This more seaward level of mean high-water spring is a damper and cooler environment than an equivalent level at the top of the beach. Thus, for *Patella vulgata*, *Nucella lapillus* and *Patella depressa*, the environment is not subject to as high a temperature range as their vertical zonation would suggest.

Therefore, if we take into account not only the factor of tidal level but also the precise nature of the habitat of each of the eleven species, there is a definite correlation between the thermal resistance of a species and the temperature range which it experiences on the shore.

SUMMARY

1. The work of previous authors on thermal death points of marine and intertidal animals is surveyed, and the relationship between the temperatures of heat death in the laboratory and the temperature ranges experienced by the species in nature is discussed.

2. The first part of the work includes the determination of the thermal death points of the eleven species when submerged. The effect of the rate of heating on the ultimate death point is considered, and demonstrated in the case of the three species of *Patella*. Using a scale of 1° C./5 min., the behaviour of the molluscs during heating is described, and the thermal death points are obtained. These are compared with temperature readings recorded on the shore, and it is concluded that heat death among the species in nature is extremely improbable. There is no apparent correlation between the thermal death points of the various snails and their vertical zonation.

3. The survival times of the molluscs at 30, 35 and 40° C. are obtained. Here again the safety limit is high, obviating the possibility of heat death in nature.

4. It is concluded that temperature acting as an isolated factor can have no direct limiting effect on the vertical distribution of the eleven species either on open rock or in tide pools.

5. The thermal death points are considered in relation to tidal level and type of habitat, and it is shown that the degree of heat-tolerance of each species is apparently related to the temperature range which it experiences in nature.

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CORIXIDAE (HEMIPTERA) AS FOOD OF FISH

By W. E. FROST and T. T. MACAN
Laboratory of the Freshwater Biological Association, Wray Castle, Ambleside

Dr E. J. Popham has recently described a series of laboratory experiments in which fish ate Corixidae. It seems of interest to examine the extensive records available at the laboratory of the Freshwater Biological Association to discover how many Corixids are eaten by fish in the wild state.

Popham (1942) observes that Corixids of one species vary in colour, and that in six ponds *Corixa* (*Arctocorisa*) *distincta* (Fieb.) tended to match the bottom. Specimens placed in an aquarium on a bottom which they did not match became restless, and attempted to fly away. Colour was measured against the grey standards of the Ostwald colour chart. In a further paper Popham (1943*b*) showed that other species tended to occur on a background which they matched, and also that the colour of the substratum influenced the development of pigment in the young stages. In an ingenious series of experiments, most of which are described in a third paper (1943*a*), it was shown that rudd (*Scardinius erythrophthalmus* (L.)) in an aquarium would feed readily on Corixidae, and tended to select those which did not match the background.

Popham (1944) then carried out an experiment in a natural piece of water, Wilpshire Quarry Pond. It contained three species, *Corixa* (*Sigara*) *venusta* (D. & S.), *C.* (*S.*) *praeusta* (Fieb.), and *C.* (*S.*) *distincta*, and no fish. After minnows had been introduced the proportion of examples of each species not matching the background was smaller than it had been previously. Various possibilities are examined, and it is concluded that the minnows had eaten the Corixids not matching the background. But no minnows were recaptured, and it was merely assumed that they had eaten Corixids; the findings of the present authors, put forward later, suggest that the failure to establish definitely that the minnows had fed on Corixids was unfortunate. Nor can we agree with the statement that Corixids migrate singly and not in large numbers (see Macan, 1939), and so we cannot accept as proven the contention that the changes observed were not due to the emigration of those species which did not match the background.

The present paper has nothing specific to add to the study of selection by fish of Corixids not matching their background, but before the full significance of the wider issues raised by Popham's laboratory findings can be assessed, some information about the extent to which wild fish prey on natural Corixid populations is essential. The present paper aims to supply this information.

Table 1 gives the data and also the sources from which they were taken. Many papers on the food of fish do not give those details which the present study requires, but the Freshwater Biological Association, which has sponsored much of the work on the subject,

Table 1. *Records of Corixidae in fish stomachs*

Species of fish	Locality	No. of fish examined	No. with food in stomach	No. of fish containing Corixidae	Total no. of Corixidae	Source of information
Brown trout (*Salmo trutta* L.)	Windermere, WL	339	—	2*	2	Allen (1938, MS. records)
		140	—	0	0	Frost (unpub.)
	Haweswater, WL	52	52	0	0	Frost (unpub.)
		103	102	†	—	Swynnerton & Worthington (1940)
	Esthwaite Water, WL	10	10	2	6	Frost (unpub.)
		7	7	0	0	Allen (unpub.)
	Three Dubs Tarn, WL	159	155	18	33	Frost (unpub.)
	Five similar tarns, WL	36	36	8	48	Frost (unpub.)
	R. Avon, Hants	137	137	24	38	Soong (1939)
	Rivers in East Anglia	37	—	5	—	Hartley (unpub.)
	Irish lakes	140	123	3	3	Southern (1935)
		231	221	30	49+	Frost & Southern (unpub.)

Table 1 (*continued*)

Species of fish	Locality	No. of fish examined	No. with food in stomach	No. of fish containing Corixidae	Total no. of Corixidae	Source of information
	Irish rivers	755	755	19	19+	Frost (1939)
		107	106	4	5+	Frost & Southern (unpub.)
	Five Scottish lochs	41	40	1	1	Frost (unpub.)
	R. Forss, Caithness	113	113	7	8	Frost (unpub.)
Rainbow trout (*Salmo irideus* Gibbons)	Wraymires Fish-ponds, WL	20	20	10	28	Frost (unpub.)
	East Anglia	1	1	1	—	Hartley (unpub.)
	L. Shure, Co. Donegal	24	24	1	1	Frost (1940)
Salmon smolts and parr (*Salmo salar* L.)	R. Avon, Hants	85	80	4	4	Moon (1937)
		17	17	9	16	Soong (1939)
	R. Forss, Caithness	136	136	4	4	Frost (unpub.)
Char (*Salvelinus alpinus* (L.))	Four lakes in Lake District	*c.* 1000	—	0	0	Frost (unpub.)
Schelly (*Coregonus clupeoides stigmaticus* Regan)	Haweswater, WL	10	10	0	0	Swynnerton & Worthington (1940)
		37	27	0	0	Frost (unpub.)
Perch (*Perca fluviatilis* L.)	Windermere, WL	643	643	0	0	Allen (1935, MS. records)
	Haweswater, WL	58	58	0	0	Swynnerton & Worthington (1940)
		4	4	0	0	Frost (unpub.)
	East Anglia	*c.* 200	—	9	—	Hartley (1947)
Eel (*Anguilla anguilla* (L.))	Windermere, WL	106	106	0	0	Frost (1946)
	Two rivers of Lake District	134	134	3	2+	Frost (1946)‡
	East Anglia	133	—	0	0	Hartley (1940 and unpub.)
Minnow (*Phoxinus phoxinus* (L.))	Windermere, WL	1228	1228	0	0	Frost (1943)
	R. Brathay, WL	833	833	0	0	Frost (1943)
	East Anglia	138	—	1	—	Hartley (1940 and unpub.)
Pike (*Esox lucius* L.)	Windermere, WL	103	71	0	0	Allen (1938)
		Over 2500	—	0	0	Frost (unpub.)
Gudgeon (*Gobio gobio* (L.))	East Anglia	*c.* 500	—	0	—	Hartley (1940, 1947 and unpub.)
Dace (*Leuciscus leuciscus* (L.))		*c.* 220	—	5	—	
Rudd (*Scardinius erythrophthalmus* L.)		257	—	3	—	
Roach (*Rutilus rutilus* (L.))		*c.* 2200	—	10	—	
Bleak (*Alburnus alburnus* (L.))		8	—	1	—	
Bream (*Abramis brama* (L.))		*c.* 1150	—	2	—	
White bream (*Blicca bjoernka* (L.))		*c.* 100	—	1	—	
Ruffe (*Acerina cernua* (L.))		*c.* 200	—	0	—	
Three-spined stickle-back (*Gasterosteus aculeatus* L.)		231	—	2	—	

* There were 13 insects recorded as 'Heteroptera'; no other indication of identity is given but there is reason to believe that bugs of terrestrial origin were referred to.

† We were unable to find the manuscript records of this work. In the published table *Micronecta* constituted 8 % of the food of 10 trout 10–15 cm. long, 0·5 % of the food of 58 trout 15–20 cm. long and did not occur in 34 trout more than 20 cm. long. The figures are arrived at by a system involving an arbitrary award of points, according to the size of the animal.

‡ In Table 7 (Frost, 1946) last column should read Cunsey Beck not River Leven.

has preserved the original manuscript records and it is on these that the figures in the table are based, although a reference is included also. Our former colleague, Mr P. H. T. Hartley, extracted for us data on Corixids in fish stomachs obtained during the course of his extensive observations in East Anglia, and we are glad to take this opportunity to thank him.

In Table 1, 18 species of fish are taken one by one, and for each is shown the number examined, the number which had fed, the number which contained Corixids, and the total number of Corixids devoured.

As a preliminary step the variation in the number of Corixids eaten from month to month is examined. Table 2 presents the results for the brown trout (*Salmo trutta*) which, as may be seen from Table 1, takes more Corixids than any other fish. It is not possible to make use of all the records for this species as some do not include the month when the observation was made.

There is a rise from March to May, then a drop to July, the total number of fish examined in August is so small that conclusions cannot be based on it, and then there is another rise in September. The difference between the figures for May and July is highly significant when the χ^2 test is applied. Records for the winter are few, and the differences between the figures for February compared with April, and for December compared with October are not significant.

There is no obvious explanation why more Corixids should be eaten in May than in the two preceding months. These insects, which must swim to the surface to obtain air, are presumably becoming more active as the temperature rises and also, perhaps, in connexion with mating which takes place at this time, and this may be the reason; or Popham's observations may provide the answer, for both Walton (1943) and Macan (1939) suggest that Corixids fly from one pond to another during the spring and early summer so there should be more species not matching their background at this time. The decrease in June and July corresponds with a period when the number of adults is falling, and the population is made up chiefly of nymphs. It is likely that these small objects are eaten less readily by fish, but the lower figure may be accounted for, in part at least, by the greater rapidity with which a nymph becomes unrecognizable in a fish stomach; the elytra of the adults are conspicuous among the contents of a fish stomach and they evidently persist unaltered for a relatively long time. The autumn rise corresponds with the gradual increase in the number of adults, and October is their main month for flying from pond to pond according to Walton (1943).

All the coarse fish were taken in traps or with a seine. The majority of the trout from Windermere, Esthwaite Water and Haweswater were caught with a seine or gill net and so were a few of the rest, though most of them were caught on rod and line. In no one body of water is there a good series of both rod and net captures, and it is not, therefore, possible to ascertain if there is a significant difference in the Corixid content of rod-caught and net-caught fish.

The results may now be discussed. Table 1 shows that only a small proportion of trout, usually less than 10%, have been taking Corixids, and the percentage of coarse fish is smaller still. The number of Corixids eaten is also very small. Trout have a habit of concentrating on one animal at a time and it is common to find a trout stomach packed with a single species (Allen, 1938; Frost, 1939). But only one of the trout stomachs examined was ever packed with Corixids and that pertained to a specimen taken from a small pool left behind after a tarn had been drained. The Corixid population of the tarn was concentrated in the pool, and the inclusion of several fish taken on this occasion is the reason why the figures for brown trout in 'five similar tarns', and for rainbow trout in Wray Mires Fishponds in Table 1 are so high. Not one of the stomachs of the coarse fish contained more than a few Corixids.

But the significance of these observations cannot be judged without some knowledge about the density of the Corixid population available for the fish to feed on. No survey was made in East Anglia, but Mr Hartley was of the opinion that Corixids occurred at most, if not all, of the stations at which he took fish,

Table 2. *Percentage of brown trout containing Corixids and number of Corixids per trout in each month*

	Jan.	Feb.	Mar.	Apr.	May	June
No. of fish examined	0	13	43	151	90	107
Percentage of fish containing Corixids	—	—	2·3	11·3	13·3	9·3
No. of Corixids per fish	—	—	0·09	0·16	0·32	0·13

	July	Aug.	Sept.	Oct.	Nov.	Dec.
No. of fish examined	116	19	179	10	0	25
Percentage of fish containing Corixids	3·4	5·2	10·6	30	—	0
No. of Corixids per fish	0·07	0·05	0·18	0·6	—	0

and at some they were certainly abundant. Nor is there precise information from the Irish and Scottish lakes and rivers. Much more is known about the Corixid fauna of the Lake District waters. In the large lakes, Windermere, Esthwaite Water and Haweswater, Corixidae, apart from the very small *Micronecta*, are almost entirely confined to reed-beds and, accordingly, restricted to a small fraction of the shallow water region of the lake. Only minnows forage in large numbers in reed-beds and, therefore, it is to be expected that all the other fish should not have fed on Corixids. In tarns, on the other hand, these bugs are an important item in the available invertebrate fauna. Three Dubs Tarn, a fishpond a little under 4 acres in extent, was under observation from 1937 to 1941 and collections in the vegetation in the shallow-water region were made in March and July annually with a hand grab covering 1 sq.ft. The different animals present in the tarn varied greatly in number from one catch to another, and it is difficult to assess their actual or relative abundance at all accurately. Corixids were more abundant in a fairly sheltered bay than along a more exposed stretch; the commonest submerged plant, *Apium*, was the same at both, but the bay was more protected by a growth of *Equisetum*. These two places should be treated separately and a distinction must be made between collections at different times of year, for in March the population is near its lowest level just before the breeding season, and in July, when the catch is mostly nymphs, it is near its peak. The results of collections separated in this way are shown in Table 3.

Table 3. *Faunistic collections with a hand grab covering 1 sq.ft. in Three Dubs Tarn*

	March		July	
	Exposed station	Bay	Exposed station	Bay
No. of hauls ...	4	5	11	3
Coleoptera	1	3	8	2
Odonata	25	4	60	17
Trichoptera	29	36	43	6
Leptophlebia (Ephemeroptera)	52	191	—	—
Others	1	33	17	15
Total of above	108	267	128	40
Corixids	18	185	126	96
Total	126	452	254	136
Av. no. of animals per haul	31	90	23	45

Small animals such as Cladocera are ignored, and no account is taken of the fauna of the mud. 'Others' include *Limnaea pereger* (Müll.) (Mollusca), *Gammarus* (Crustacea), Leeches (Hirudinea), *Nemoura* (Plecoptera), and *Cloëon* (Ephemeroptera). The beetles were all small, *Haliplus fulvus* (Fab.) being the most abundant. The Odonata were nearly all Coenagriids, though a few Aeshnids and Libellulids occurred in the July collections. *Cyrnus*, a Polycentropid, of which the larva has no case, was the commonest Trichopteron; others were a *Leptocerus* with a stony case, a *Limnophilus* and a *Phryganea* both with a vegetable case, and a swimming larva *Triaenodes*. The Corixids were nearly all *Corixa scotti* (Fieb.).

In July the number of Corixids at the exposed station was equal to that of all the rest of the fauna put together, and in the bay it was more than double. In March, at the exposed station Corixids were rather scarce, but in the bay the number per grab was approximately the same as it had been in July, and here Corixids vied with *Leptophlebia* as the most abundant animal. The *Leptophlebia* nymphs began to emerge in May, and had disappeared completely by the end of June. Though there is no exact ratio to be deduced from these figures it can safely be asserted that Corixids were one of the commonest animals available for the fish to eat. Apart from the beetles, of which the numbers were insignificant in comparison, they were the only animals which visited the surface for respiration, an activity which, it might be supposed, would lay them more open than other members of the fauna to predatory attacks of fish.

This fauna was typical of the vegetation. A great part of the tarn was without vegetation during the period in question, and away from the weeds the fauna available for the fish to eat was either plankton or bottom fauna, which comprised Chironomid larvae, *Pisidium*, Oligochaetes, *Sialis* (Megalopt.) larvae, and *Caenis* (Ephem.) nymphs. The numbers of these various animals found in trout stomachs are shown in Table 4.

From the data it may be concluded first, that the fish did feed in the vegetation where the Corixids occurred, and secondly, that the numbers of Corixids which they took were small when compared with the numbers present.

It would seem, then, that a wide range of freshwater fish from a wide range of habitats take Corixids in much smaller numbers than would be expected if they were feeding at random off what is available. But this is not an invariable finding. Van Someren (1939) records trout stomachs containing many Corixidae. On Barra, one of the Outer Hebrides, he investigated a small moorland loch with clear brown peaty water. The fauna was mainly Corixids and *Pisidium*. Brown trout caught in this loch contained 55·6% Corixids, the species being *Corixa scotti* and *Cymatia bonsdorffi* (Sahlb.), according to the published account; in a letter to one of the authors Dr van Someren mentioned a fish in which 90% of the stomach contents was Corixids. He proceeds further

in his paper: 'On several other lochs I have noticed this extensive feeding on Corixids, . . . particularly in a small lake I fished for two years in Surrey.'

Frost has a record of a few sea trout feeding extensively on Corixids. They were in a small peaty lough cut off from the sea by a sand bank though liable to invasion at high-water springs or during stormy weather. This place was also without rooted vegetation, and the opinion was formed that the fish were feeding on Corixids because there was nothing else to eat. Van Someren's observations would support this argument, but it is not always applicable, for Walton (1943, p. 268) records 62 Corixids from the stomach of a trout in Blagdon Reservoir, and we learn from Mr C. Myers that in this piece of water trout prey extensively on Corixids though other animals are abundant. However, these exceptions do not invalidate the general assertion which is based on data from many different places.

food fauna. How far the specimens eaten are those which do not match the substratum is not known. Selection may take place even though the numbers of an organism destroyed are small, and there is no reason to doubt that it is operating in the present instance. But the pressure of fish on Corixid populations would appear to be much less than aquarium experiments indicate.

SUMMARY

1. In a series of papers Popham has shown that several species of Corixidae vary in colour. In an aquarium Corixids are eaten readily by fish, and those which do not harmonize with the background tend to be selected more than those which do.

2. An attempt to interpret field observations along the same lines is challenged. Changes in the Corixid population of a pond are attributed by Popham to minnows which eat Corixids in an aquarium. But over a thousand minnows from Windermere had not eaten a single Corixid, though this fish seeks food in reed-beds, where Corixids are numerous.

3. Records of the number of individuals eating Corixids, and of the total number of Corixids eaten, for large samples of 18 species of fish, are presented (Table 1).

4. Few fish had taken Corixids, and only in exceptional circumstances had any one fish devoured a large number of Corixids.

5. Seasonal variation in the consumption of Corixids (Table 2) is discussed.

6. In a fishpond, where extensive observations on the fauna and on the food of fish have been made, it is found that the number of Corixids taken is low when compared with the proportion in the fauna.

7. Records of the few occasions when fish have been found feeding readily on Corixids are given.

Table 4. *Numbers of the animals found in the stomachs of brown trout caught in Three Dubs Tarn*

	Food organisms	Mar.–May	June, July	Aug., Sept.	Total
Weed fauna	Aquatic Coleoptera	4	1	2	7
	Odonata nymphs	36	5	9	50
	Trichoptera larvae	395	131	71	597
	Leptophlebia nymphs (Ephem.)	88	—	—	88
	Others (*Limnaea*, *Gammarus*, *Cloëon*)	21	11	22	54
	Corixids	14	8	11	33
Bottom fauna	*Sialis* larvae (Megalopt.)	175	—	26	201
	Caenis nymphs (Ephemeropt.)	—	160+	—	160+
	Chironomid larvae	145	55	54	254
	Pisidium	111+	2	41	144+
Plankton	Chironomid pupae	298+	75+	117	490+
Animals taken at the surface	—	86+	68+	252+	406+

Corixidae, like nearly all other members of the order, have glands which secrete a noxious substance. Whether they are avoided by fish on this account has not been investigated. Three surface-dwelling genera, *Velia*, *Gerris* and *Hydrometra* which do not possess such glands (Weber, 1930) are taken even less often than Corixidae and this is unexpected, at least for the trout which, at certain times of the year, obtains a considerable amount of its food at the surface (Table 4).

The literature on the food of birds has not been searched, but worthy of note here is a manuscript record by Mr P. H. T. Hartley who shot a hen shoveller (*Spatula clypeata*) in Cambridgeshire and found that it had been feeding extensively on Corixids. Berry (1935) records finding numbers of Corixids in 15 mute swans (*Cygnus olor*) which he shot in Fife.

The conclusion is that, in general, the number of Corixids eaten by fish is small and the proportion low when compared with the proportion in the available

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THE ECOLOGY OF SALDIDAE (HEMIPTERA-HETEROPTERA) INHABITING A SALT MARSH, WITH OBSERVATIONS ON THE EVOLUTION OF AQUATIC HABITS IN INSECTS

By E. S. BROWN

(With 1 Figure in the Text)

1. INTRODUCTION

The Saldidae are a family of insects belonging to the Hemiptera-Heteroptera, of particular interest in that the species show varying tendencies towards aquatic life; if the habits of all the species were worked out in detail, a great number of the stages in a graded series between completely terrestrial and almost completely aquatic existence could probably be represented, each by one or more species of these insects. *Saldula orthochila* (Fieb.), at one end of the scale, normally inhabits dry ground; the majority of species live in damp situations, such as on the wet mud at the margins of ponds and streams, and in the *Sphagnum* surrounding bog-pools; other species inhabit the seashore, and there is some evidence that these tend to progress furthest in the direction of aquatic adaptation.

One must remember that insects are primitively a terrestrial group, and that the aquatic orders, families and other subgroups represent so many sporadic and separate lines of evolution each culminating in adaptation to life in water. Semi-aquatic groups such as the Saldidae and the larval stages of Tipulidae (crane-flies) are therefore of peculiar interest, as showing possible methods by which colonization of the water may have occurred, and it was partly with a view to throwing light on this aspect that the present study was undertaken. Previous work on Saldidae in this direction appears to be scanty, but a few relevant facts have been published. Mason (1889) described a tidal locality in Cornwall inhabited by *Halosalda lateralis* (Fall.) and *Saldula saltatoria* (L.), and stated that he observed these insects to be submerged by the incoming tide, and to cling to weeds or the substratum during the period of submersion. It is not clear from his account whether both species were submerged to the same extent, or whether, indeed, only one species was submerged, but *S. saltatoria* was clearly stated to have been immersed on one occasion. Renouf (1931, 1932, 1934), working in southern Ireland, has recorded some facts of particular interest concerning a tidal locality inhabited by *S. pallipes* (Fab.); he states that this insect skates on the surface of pools, and occasionally runs across the bottom; but although he implies that this and many other species of Hemiptera became submerged, because they inhabited islands which were covered by high spring tides, he was evidently unable to produce any precise evidence that this was the case, or if it was, which species were submerged, and to what extent.

When I was investigating the aquatic Hemiptera of Anglesey in 1941 (Brown, 1943), a colony of *S. pallipes* was encountered in a tidal area, under conditions where it seemed likely that the insects might be submerged, or flooded out, at high tide. An opportunity has now presented itself to do further work in a locality in many respects similar to the one in Anglesey.

2. THE SPECIES OF SALDIDAE CONCERNED

In the areas investigated in detail, three species of Saldidae occurred: *Halosalda lateralis* (Fall.), *Saldula pallipes* (Fab.) and *S. pilosella* (Thoms.); of these the first two, and especially *S. pallipes*, were very well represented, but the numbers of *S. pilosella* were so small that the data cannot be regarded as significant for this species. *S. pallipes* was represented by a very dark form which was almost the only one occurring in the locality. This dark form was described by Douglas (1874) as a separate species, *S. palustris*, and appears as such in China's check-list of British Heteroptera (1943), and also in the check-list of Kloet & Hincks (1945); my own experience, however, indicates that dark and pale forms are only colour varieties of one species; it is intended to justify this view in a separate publication at a later date.

3. DESCRIPTION OF LOCALITIES INVESTIGATED

Most of the data were collected in August 1947, on the southern shore of the estuary of the river Stour, near Nether Hall railway station (about 2 miles east of Manningtree, in north Essex). Two areas of ground were investigated (referred to as 'A' and 'B'), both

having the same general features, but differing in small details.

Area 'A'. From the top of the beach, bounded by an overhanging bank (see Fig. 1), to the bottom there were a number of rather clearly defined zones, differentiated mainly by vegetation, occurring in the following order (described as they appeared at low tide):

(i) A belt 4 yd. wide of dry, bare sand, yielding no Saldidae.

(ii) An extent of about 6 yd. of wet, muddy sand, with small puddles and bounded above by a small quantity of rejectamenta cast up by the highest tides, but not covered by the normal high tide. The tidal rejectamenta about a yard wide, but this did not represent high-tide mark, since it was caught up in the thick vegetation; the tide extended at least part of the way up this zone.

(iv) Next came a broad belt (about 60 yd.) of soft, water-saturated mud with a thick growth of *Spartina townsendii*, which formed the dominating vegetational feature of the whole area; a little scattered *Enteromorpha* was the only other plant; small patches of bare, unvegetated mud accounted for approximately one-tenth of the ground area. Crabs, and the prawn *Palaemonetes*, were common, but Saldidae only occurred in the upper part.

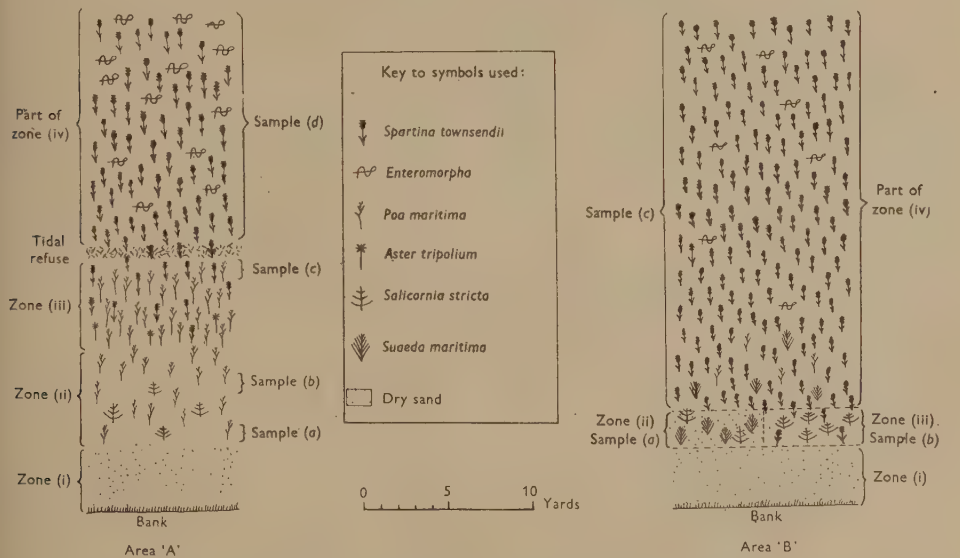

Fig. 1. Diagram of areas 'A' and 'B' in the Nether Hall locality, showing the zoning of the larger plants in those parts inhabited by Saldidae, and the places where sample collections were taken.

vegetation was rather sparse, consisting mainly of *Poa maritima*, with a few scattered plants of *Salicornia stricta* (= *europaea*), and small patches of a filamentous green alga (*Rhizoclonium* sp.) growing on the damp soil. A few small crabs were to be found towards the bottom of this zone, and Saldidae were particularly abundant.

(iii) This belt, also about 6 yd. wide, differed from the one above it only in being rather wetter, and in incorporating a little *Spartina townsendii* in its flora, as well as a few scattered plants of *Aster tripolium*; *Salicornia* was absent, but the vegetation generally was slightly thicker. There were more crabs, and Saldidae were by contrast less common, although well represented. At the bottom of this zone was a belt of

(v) Below the *Spartina* zone, bare mud, with a little *Enteromorpha*, extended as far as the water's edge.

Area 'B'. This was about half a mile east of 'A', and similar to it in main features (see Fig. 1), with a number of distinct zones as follows:

(i) A belt of dry, bare sand, without any Saldidae identical with the corresponding zone in 'A'.

The next belt, 2 yd. wide, was not uniform, and may be divided into two (zones (ii) and (iii)), as indicated in Fig. 1.

(ii) This was a strip about 8 yd. long, slightly more elevated and of rather dry, sandy gravel, pale in colour; the vegetation, consisting principally of *Suaeda maritima*, and with scattered plants of *Salicornia stricta*, *Poa maritima*, *Atriplex patula* and

Spergularia salina, was sparse, covering only about one-tenth of the ground.

(iii) A longer neighbouring strip was about 1 ft. lower in elevation, and the soil was wetter and darker in colour; it was only slightly less thinly vegetated, the flora containing *Salicornia stricta* (dominant) and *Spartina townsendii* (scarce); a trifling quantity of tidal refuse lay on the soil.

(iv) Next came a broad belt of wet mud thickly covered with *S. townsendii*, corresponding precisely with zone (iv) in area 'A'.

4. THE DISTRIBUTION OF THE SPECIES OF SALDIDAE

Collections of Saldidae were made with a 'haustorium' from each of the strips (*a*), (*b*), etc. (as indicated in Fig. 1), until sufficient had been obtained for a count to be significant. The results are summed up in Table 1. Two salient facts emerge from these figures.

(1) So far as *Halosalda lateralis* and *Saldula pallipes* are concerned there is a clear zoning of the species, the former being restricted to the top of the intertidal zone, and the latter extending much farther down where conditions are wetter.

(2) *Saldula pallipes* extends its range far down on to ground which is well and truly submerged at high tide. In area 'A' examples occurred up to 15 yd. below the top of zone (iv), and in area 'B' as much as 30 yd. below the top of the same zone. This immediately raises the question as to what happens at the rise of the tide; do the Saldidae retreat before it, or do they become submerged? This will be answered in the next section.

5. THE ZONING OF ADULTS AND NYMPHS, AND SUBMERSION AT HIGH TIDE

While samples were being taken it immediately became apparent that, in the most abundant species *S. pallipes*, the distribution of adults and nymphs was very uneven, in that the former were relatively more abundant about the high-tide mark, and the nymphs more abundant farther down. Separate counts of adults and nymphs (Table 2) confirm the increase in the percentage of nymphs as one passes down the beach in both areas 'A' and 'B'.

This fact lent added interest to the whole investigation. It would, *prima facie*, occur to one that the nymphs, being more delicate, would be less likely than the adults to penetrate the intertidal zone and risk the dangers of submersion. It therefore became all the more desirable to ascertain if, and to what extent, these insects became submerged at high tide. Accordingly certain points at or near the bottom of the zones inhabited by Saldidae, and which would be overrun by the tide, were marked with tall sticks; one such point was marked in area 'A', and another in area 'B', respectively 10 and 25 yd. below the top of zone (iv); they were selected because they supported plenty of Saldidae at low tide. When these points were well covered by the incoming tide, to a depth of a foot or more, they were worked with a water net. The point in area 'A' yielded one adult and nine nymphs of *Saldula pallipes*, while that in area 'B' yielded ten adults and forty-five nymphs, each sample being the result of only two or three workings of the net. It was carefully noted that the insects were caught by working the net amongst the weeds on the bottom; the *Spartina*, which was the dominant plant, was partly emergent when the collections were made, but the insects were not on the emergent parts, but at the bottom and completely submerged. Thus not only was it established that both nymphs and adults are submerged by the tide for at least 2 or 3 hr. (time unfortunately did not allow an exact estimate of the submersion period to be made), but that nymphs probably tend to submerge more readily than adults, for the proportion of nymphs was higher in these samples than in those made on the same ground at low tide. It is therefore possible that some of the adults retreat before the advancing tide, and that all the nymphs remain where they are, though it would be necessary to investigate more carefully to substantiate this.

6. EVIDENCE FROM OTHER LOCALITIES

So far as the zoning of species is concerned, some confirmatory evidence was obtained from a much more thinly populated Saldid colony on the north shore of the same estuary, near Brantham (east Suffolk). The terrain here was similar, except that the slope was steeper, and the intertidal zone therefore narrower. In this instance Saldidae were only found about the high-tide mark, and did not extend down into the intertidal zone more than 2 or 3 yd., and even then they were scarce. For sample counts, a dividing line was selected above which no small puddles of standing water remained at low tide, and which therefore represented approximately the high-tide mark; samples of the Saldidae were collected from two strips, each about 2 yd. wide, one of them above and the other below the selected line. The vegetation was rather thicker than in the corresponding part of the Nether Hall locality; plants common to both upper and lower strips were *Poa maritima* (dominant), *Salicornia stricta*, *Suaeda maritima*, and the filamentous alga *Rhizoclonium*; in the upper strip there appeared also *Obione portulacoides*, *Plantago maritima*, *Spergularia salina* and *Limonium vulgare*; in the lower strip was a little *Aster tripolium* and *Triglochin maritima*; and farther down the vegetation passed into a thick growth of *Spartina townsendii*, as in the Nether

Hall locality. The samples of Saldidae from the two strips were as follows:

	Halosalda lateralis	*Saldula pilosella*	*Saldula pallipes*
Above high-tide mark	14	1	75
Below high-tide mark	0	0	10

These figures, although small, support the evidence from Nether Hall in indicating that *Saldula pallipes* is more inclined than *Halosalda lateralis* to invade the salt marshes at Dovercourt were *Chiloxanthus pilosus* (Fall.) and *Salda littoralis* (L.).

A species which seems only rarely to occur in tidal areas is *Saldula saltatoria*, which is the commonest Saldid in the British Isles generally. Mason's account (1889) of the submersion of this species by the tide is therefore somewhat surprising, and raises a suspicion that it might have been a dark form of *S. pallipes* that he observed. It is to be noted that although *S. saltatoria* existed at the margin of a pond within a few

Table 1. *The numbers of Saldidae in the samples taken from areas 'A' and 'B' of the Nether Hall locality. For locations of zones, and of samples, see Fig.* 1

(N.B. Owing to the sampling methods used, the total numbers for different zones are not strictly comparable, but the relative numbers of the three species in each zone are significant).

	Area 'A'				Area 'B'			
Zone	Location of sample	*Halosalda lateralis*	*Saldula pilosella*	*Saldula pallipes*	Location of sample	*Halosalda lateralis*	*Saldula pilosella*	*Saldula pallipes*
(ii)	(*a*)	3	—	105	(*a*)	17	—	9
	(*b*)	—	3	100	—	—	—	—
(iii)	(*c*)	—	—	82	(*b*)	19	—	54
(iv)	(*d*)	—	—	67	(*c*)	—	—	79

	Areas 'A' and 'B' combined		
Zone	*Halosalda lateralis* (%)	*Saldula pilosella* (%)	*Saldula pallipes* (%)
(ii)	9	1	90
(iii)	12	0	88
(iv)	0	0	100

Table 2. *The numbers and percentages of adults and nymphs of* Saldula pallipes *at different levels on the beach in the Nether Hall locality. For locations of zones, and of samples, see Fig.* 1

	Area 'A'					Area 'B'				
		Adults		Nymphs			Adults		Nymphs	
Zone	Location of sample	Actual no.	%	Actual no.	%	Location of sample	Actual no.	%	Actual no.	%
(ii)	(*a*)	97	92·4	8	7·6	(*a*)	9	100	0	0
	(*b*)	78	78·0	22	22·0	—	—	—	—	—
(iii)	(*c*)	56	68·3	26	31·7	(*b*)	46	85	8	15
(iv)	(*d*)	18	27·0	49	73·0	(*c*)	31	39·2	48	60·8

tidal area. The adult-nymph ratios in this instance, however, are insufficient to be significant.

As regards *Saldula pilosella*, additional data are scanty and rather conflicting. In an extensive salt marsh at Dovercourt (north Essex) it was found in two places: on algae floating on a small salt pool which was probably not reached by the tide, and, with *S. pallipes*, on flats which were probably under tidal influence. Again, it occurred with *S. saltatoria* at the margin of a fresh-water pond about 100 yd. from area 'A' at Nether Hall. Other Saldidae occurring in the yards of the Nether Hall locality (as mentioned above), it did not occur in the intertidal zone.

7. SUBMERSION EXPERIMENTS

Since the data from the field work indicated that the distribution of *Halosalda lateralis* and *Saldula pallipes*, and of adults and nymphs in the case of the latter species, might be related to a difference in their ability to withstand submersion, it was decided to put this matter to the test by experiment in the laboratory.

Unfortunately, insufficient living material of *S. pilosella* was available, when this decision was made, to include this species in these experiments.

For submersion, fresh water was used instead of sea water, since the latter was not available; it is unlikely that this would affect the results to any significant extent. The apparatus consisted of glass tubes (6 × 1 in.), into each of which could be inserted a platform of muslin stretched on a wire ring, which fitted exactly the internal diameter of the tube; Saldidae could thus be placed in the tube with water, and then forced beneath the surface, and trapped there, by lowering the muslin platform on to the top of them; they were thus withheld from communication with the atmosphere for any desired period. The tubes were all of the same size, and the same quantity of water was used in each case; since this water always came from the same source, the oxygen content must have been identical, or nearly so, in all tubes.

In a first experiment, ten Saldidae were placed in each of five tubes; two contained adult *S. pallipes*, two adult *Halosalda lateralis* and the other nymphs of *Saldula pallipes*; a small quantity of a filamentous alga was put into each as a foothold, but when water was introduced into the tube the insects nearly all floated to the top and clung, inverted, to the muslin which kept them beneath the surface.

The behaviour of the Saldidae on their enforced submersion was in the main outline similar in all cases. They rested, or crawled about, on the undersurface of the muslin, or on the alga in the case of the few which clung to it. More or less of an air-film or series of air-bubbles surrounded their bodies, and some part of this air-store must have been in communication with the spiracles in the majority of cases; after a time the air-store dwindled, and sooner or later they became less active, their legs flexed under their bodies, and they entered into a condition of torpor and appeared to be dead, showing no signs of movement even when prodded with a needle through the muslin; in most cases, however, it was found that they were not dead, for when removed from the water and dried they generally recovered, provided they had not been in a state of torpor for too long.

There were, however, important differences between the different Saldidae in the details. As regards the air-film, the adult *S. pallipes*, having a coating of short hydrofuge hairs, retained a good air-store in the form of a large bubble on the upper surface of the elytra and thorax, or on the underside of the abdomen (sometimes both), and in many cases a large bubble was entrapped under the elytra. The *Halosalda lateralis*, having a smooth surface, did not usually retain such a large air-store, but often had a large bubble under the elytra, supplemented by a few small ones on the outer surface. The nymphs of *Saldula pallipes*, having of course no elytra, and a surface mainly smooth, retained hardly any air by comparison with the adults. In behaviour there was a marked difference between *S. pallipes* and *Halosalda lateralis*. The latter became restless at once on submersion, most of them hurrying about as if endeavouring to find a way of escape; the *Saldula pallipes*, by contrast, either remained at rest, or moved about in a leisurely manner, giving one the impression that it was in their nature to be submerged. The *Halosalda lateralis* began to reach a state of torpor in a quarter of an hour, and after 35 min. all were in this condition; however, after 2½ hr. they were removed, and 50 min. later all had recovered. The *Saldula pallipes*, on the other hand, remained active for a much longer period; in the two tubes containing adults, it was 1½ hr. before any reached a torpid condition, and only half had done so after 4 hr.; they were then left submerged overnight, and the next morning, after nearly 14 hr. submersion, all were torpid; but on removal to dry tubes, twelve out of the total of twenty recovered in a few hours. The single tube of *S. pallipes* nymphs gave an even better performance; after the initial submersion, all ten nymphs remained active at the end of 4 hr., when they were left overnight; the next morning, after nearly 14 hr. continuous submersion, three were still active, and on removal to a dry tube every one recovered after 3½ hr. On the other hand, of the twenty *Halosalda lateralis* (two tubes) which had been removed, and had recovered, ten were replaced in water and left submerged overnight; the next morning all were torpid, and on removal only two eventually recovered.

These results are remarkable in certain respects, and are very well in accordance with what one might expect from the distribution of the insects in nature with respect to the tide. To confirm the results, a second experiment was done on similar lines. This time six tubes were used, five insects being placed in each; two contained adult *Saldula pallipes*, two contained nymphs of *S. pallipes* and the remaining two adult *Halosalda lateralis*. No alga was included in the tubes on this occasion, since in the first experiment small bubbles of gas given off from these plants (oxygen resulting from photosynthesis) may have had some slight effect on the results. The behaviour of the insects on submersion was the same as in the first experiment, the *H. lateralis* becoming very restless immediately, and the *Saldula pallipes* moving slowly about or remaining still.

As regards the difference between the species, and between adults and nymphs, in subsequent events, there was enough similarity to the previous results to confirm them. The *Halosalda lateralis* did not become torpid so early as they had done on the first occasion, but were nearly all in this state after 1 hr., whereas after the same interval all except one adult and one nymph of *Saldula pallipes* were still active. After

3½ hr. (probably before, but there was a gap in observations) all the *lateralis* were torpid, but only four adults and three nymphs of *S. pallipes*; thus up to this point there was little difference between the adults and nymphs of *S. pallipes*; however 2 hr. later eight adults, but only four nymphs had succumbed.

Since there were two tubes of each type of Saldid, it was possible henceforth to subject each type to two different courses of treatment. From one tube of each the insects were extracted and placed in dry tubes, to see how far recovery would take place after 5½ hr. submersion; four of the five recovered in both adults and nymphs of *S. pallipes*, and *all* the *lateralis*—a result not quite in accordance with what was expected, but it is significant that those *pallipes* which recovered did so much more rapidly than the *lateralis*.

In the remaining tubes the Saldidae were kept submerged until 10.15 p.m., that is to say, for a total of 10¾ hr., by which time one *pallipes* adult, and three nymphs were still active, while all the *lateralis* had been torpid for hours; all the insects were then removed to dry tubes, and the *lateralis* failed to recover altogether, while three adults and four nymphs of *pallipes* were once more active after ¾ hr., and one more adult was found to have recuperated the next morning.

These experiments taken in conjunction, although limited in number, enable one to make with some confidence two interesting conclusions:

(1) That *Saldula pallipes* can withstand submersion longer than *Halosalda lateralis*, and has a greater and more rapidly operating power of recuperation from the torpor which submersion eventually induces.

(2) In *Saldula pallipes*, the nymphs can withstand submersion longer than adults.

Both of these facts are in agreement with what one would expect from the distribution and behaviour of these insects in nature.

8. THE EFFECT OF DESICCATION ON ADULTS AND NYMPHS OF *SALDULA PALLIPES*

Since nymphs of *S. pallipes* tend to inhabit wetter situations than the adults, a chance observation on the effects of desiccation is worth recording. Samples from a number of zones of the Nether Hall salt marsh, each containing both adults and nymphs, were taken home alive in glass-topped cardboard boxes, in which the conditions were much drier than in their natural habitat. After a time many of the insects were found to have died, and it was noted that death usually occurred sooner in the nymphs than in the adults, as the following figures for different boxes will show:

Period of imprisonment in box (hr.)	Adults		Nymphs	
	Alive	Dead	Alive	Dead
46½	57	2	8	22
48	6	91	0	8
48	8	1	4	7
49½	36	42	0	21
70	8	16	0	36
80	11	45	0	2

It seems probable from this that nymphs are more susceptible to desiccation than adults; it is true that other factors, such as lack of food, may have been involved; but in spite of this the figures are large enough to be strongly suggestive, and are therefore put on record as illustrating a possible contributory factor in distribution; the comparatively dry conditions above high-tide mark might be a greater source of danger to nymphs than to adults, having the effect of driving them down the beach to areas where, among the luxuriant growth of *Spartina*, the humidity at ground level is very high, even at low tide.

9. DISCUSSION

As far as ability to withstand submergence is concerned, the main handicap is respiration. Experiments described in this paper show that this ability in *Halosalda lateralis* adults, and in adults and nymphs of *Saldula pallipes*, varies in accordance with the different extents to which they have penetrated the intertidal zone; *S. pallipes* nymphs can withstand submergence longest, and have penetrated farthest, or at least, to judge by relative numbers are more at home than adults at the lower limit of the range of the species. There arises therefore the question why *pallipes* nymphs can withstand submergence longer than adults, and *pallipes* adults longer than *lateralis*. This cannot as yet be answered with confidence, but one or two possible factors are indicated. As regards the adults, *pallipes* is more pilose than *lateralis*, and more readily retains external air-bubbles on submergence, especially on the upper surface of the elytra; *lateralis*, however, although it has a smooth, shiny upper surface, usually retains an air-bubble on the underside or at least under the elytra; there are indications that this factor may not be of any great importance, since preliminary experiments with two other Saldid species, *Saldula saltatoria* and *Chartoscirta cocksii* (Curtis), show that they also retain a good external air-store, but are not able to withstand submergence to anything like the same extent as *pallipes*. It must also be emphasized that the nymphs of *Saldula pallipes*, which withstand submergence longest, retain only a very few small air-bubbles externally; they have no elytra beneath which an air-store can be trapped. It is most probable that a form of branchial, or true aquatic respiration takes place here, oxygen diffusing through the general body surface from solution in water; the integument of the

nymph being more delicate than that of the adult, and more or less hydrophile, this type of respiration would operate more readily. An opinion put forward by Alluaud (1926), when summarizing the problem of submergence of littoral insects, is worth mentioning; he states that such insects probably survive submergence by making use of small quantities of air imprisoned in rock crevices, under stones etc. This may be true of the bug *Aëpophilus* and certain beetles which he was discussing in particular, but could hardly be the case in the present instance, since the area in question was a tidal mud-flat without rocks or stones, and with vegetation which would hardly imprison air on the scale necessary to support a strong Saldid population; besides, the submersion experiments described above make it clear that *Saldula pallipes* is capable of withstanding long submergence, without the help of air-stores other than the air-bubbles retained by its own body.

Another aspect of the question of resistance to submersion involves behaviour. It has been stated above that *Halosalda lateralis* become very restless and active on submergence; they would thus use up their oxygen quickly, and this no doubt explains their rapid passage into a torpid state. Both adults and nymphs of *Saldula pallipes*, on the other hand, are much less active on submergence; for the most part they remain quite motionless, and if they move from place to place do so comparatively slowly; in their natural habitat they doubtless cling to vegetation, as described by Mason (1889), or bury themselves in the mud, as indicated by the fact that several of those collected from the tidal part of the Nether Hall locality had a slight incrustation of mud on the prothorax; Mason describes occasional movement from one place to another, but inactivity is doubtless the normal thing. Such behaviour would reduce oxygen consumption to a minimum, and therefore increase the possible submergence period; and if the nymphs can supplement their air-store with some small amount of branchial respiration, as seems likely to be the case, this period would be increased still further.

We are therefore led to the interesting conclusion that *S. pallipes* is a species in the fore-front of an evolutionary tendency found in the Saldidae towards water-colonization; and that aquatic adaptation has proceeded to a greater extent in the nymphs than in the adults. Further, there are strong indications that the nymphs are in process of becoming 'true' aquatics (breathing by extracting dissolved oxygen from solution in the water), while the adults are becoming 'false' aquatics (which can only utilize gaseous, atmospheric oxygen). While this last point requires further experimental work for substantiation, it would only be a repetition of what has occurred in the evolution of other groups of aquatic insects: young stages have become 'true' aquatics, while the adults have remained terrestrial, or only succeeded in developing a 'false' aquatic organization, in Plecoptera, Ephemeroptera, Odonata, Trichoptera, and in certain Neuroptera, Lepidoptera (e.g. *Paraponyx*), Coleoptera (Gyrinidae, Psephenidae), and Diptera (Chironomidae, Simuliidae etc.). Aquatic evolution in *Saldula pallipes*, however, has not yet reached the stage when normal activities can be maintained under water, at all events for any length of time; but it would only be necessary for the nymph to improve its branchial type of respiration, for instance by developing tracheal gills, in order to achieve this final step in larval evolution. It is therefore interesting as a probable instance of incipient caenogenesis (de Beer, 1930, p. 37) in which change of habits has not yet been accompanied by morphological change; and caenogenesis has characterized aquatic adaptation in nearly every insect group which has taken to the water.

It should be mentioned, however, that there are strong indications that aquatic evolution in the Hemiptera took a rather different course in the past, from an early ancestor of Saldid type; China (1933) has traced the probable origin of many of the important living aquatic families through the littoral Saldidae, and the closely related Ochteridae and Gelastocoridae to the fully aquatic Nepidae, Belostomatidae, Naucoridae and Aphelocheiridae; and in a later paper (1940), he traces the process still further to include the Helotrephidae, Pleidae and Notonectidae; all these aquatic families except the Aphelocheiridae are generally thought to have aerial respiration in all stages, indicating a different course in evolution from that suggested above; but it is very probable that at least the larval stages supplement aerial with a greater or lesser degree of branchial respiration; such a tendency would at all events have given impetus to the initial steps in aquatic evolution, and it is possible that more recent evolutionary trends as indicated by *S. pallipes* may not be very different from the earlier ones.

A curious fact is that while recent aquatic trends in Saldidae are more conspicuous in maritime species, suggesting a tendency to colonization of the sea, the well established aquatic families of Hemiptera mentioned above are inhabitants of fresh water. It is true that they may have passed through initial stages of aquatic evolution in salt water, because an existence in the intertidal zone is more conducive to initial aquatic adaptation than one at the margins of non-tidal fresh-water bodies; but there are grave disadvantages to life in the sea from an insect's standpoint, and there are few fully adapted marine insects as compared with those inhabiting fresh water; there would thus be a strong bias towards colonization of fresh water, even if the initial stages of aquatic evolution had occurred at the margin of the sea. However,

at least one line of evolution, from a Saldid type of ancestor, has resulted in more complete adaptation to life in the sea. The marine water-bug *Aëpophilus bonnairei* Signoret, in the closely allied family Aëpophilidae, has evolved far enough to be able to withstand submergence in the sea for long periods under natural conditions. China (1927) found that in laboratory conditions it became torpid after 21¼ hr., and he suggests that it respires, after the manner of a 'true' aquatic, through its cuticle when submerged, and that it has evolved from littoral Saldidae. It could well represent a later stage in the evolutionary process indicated by *Saldula pallipes*, as discussed above, but in which, so far as is known, the adults have become adapted to aquatic respiration to the same extent as the nymphs; Alluaud's opinion that this bug gets what air it requires from stores imprisoned in rock crevices is largely discounted by China's submersion experiments. *Aëpophilus* has not undergone any modification of structure in connexion with aquatic locomotion, but this is doubtless because it is unnecessary in view of its living in rock crevices.

It is hoped that the observations here recorded will direct attention to an interesting line of investigation. There are other groups of insects which show similar tendencies towards water colonization; the Hydrophilidae and Carabidae amongst Coleoptera, and the Tipulidae amongst Diptera; in the Hemiptera, besides the Ochteridae and Gelastocoridae mentioned above, the Cryptostemmidae show an independent tendency towards water colonization; and in the Homoptera, some instances of very considerable interest have been placed on record in America by Arndt (1915), and Metcalf & Osborn (1920). These authors describe observations of some detail on several small leaf-hoppers belonging mainly to the Jassidae and Delphacidae, some of which are regularly submerged by the tide. One species (*Liburnia detecta* van Duzee) is in fact confined to the intertidal zone and is submerged for long periods. Further study of such insects, which are in the semi-aquatic stage, directed particularly towards their ability to withstand submergence, and their habits and activities while submerged, might throw an interesting light on the evolution of aquatic adaptation.

10. ACKNOWLEDGEMENTS

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11. SUMMARY

1. In an estuarine salt marsh at Nether Hall, on the southern shore of the estuary of the River Stour, there is a zoning of species of Saldidae in the intertidal area and slightly above it. *Halosalda lateralis* (Fall.) occurs on drier ground just above the high-tide mark; *Saldula pallipes* (Fab.) on the other hand, while also occurring at and above high-tide mark, extended far down into the intertidal zone, where *Halosalda lateralis* did not penetrate. There was, in addition, a clear zoning of adults and nymphs of *Saldula pallipes*, in that the latter tended to occur on the lower levels of the beach in far greater numbers. The zoning of these insects may be therefore represented as follows:

Halosalda lateralis
Saldula pallipes adults
Saldula pallipes nymphs

There was, of course, a certain amount of overlapping, as can be seen from Tables 1 and 2.

Saldula pilosella (Thoms.) also occurred in this and other habitats in the district, together with the other two species, but in insufficient numbers to provide any reliable conclusion as to the level it normally occupies in tidal areas.

Such evidence as was available from other localities was in agreement with these conclusions.

2. It was found that, at high tide, both adults and nymphs (especially the latter) of *S. pallipes* remained at the lower levels and were submerged by the rising tide, instead of retreating before it.

3. Laboratory experiments involving enforced submergence showed that *S. pallipes* was able to withstand submergence in a more or less inactive state for long periods without suffering permanent harm, and its performance in this respect was superior to that of *Halosalda lateralis*. The results were in accordance with what one would expect from the distribution of the two species in their natural habitat.

4. The probability that *Saldula pallipes* is a species in the fore-front of an evolutionary tendency towards colonization of the water from the land is discussed. Two factors apparently limit the extent of the colonization of the intertidal zone; first, the period of time for which the Saldidae can withstand submergence; and secondly, the period of activity and feeding, which is apparently (but not certainly) limited to the duration of exposure at low tide, and would become shorter and shorter as the insects penetrate farther down the beach.

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TEMPERATURE AND RATE OF DEVELOPMENT OF THE EGGS OF BRITISH ANURA

By ROY DOUGLAS

(With 3 Figures in the Text)

1. INTRODUCTION

A general account of past work on temperature in relation to amphibian morphogenesis is provided by Moore (1939), who gives also a fuller bibliography. The present paper is an attempt to apply the conclusions of his work, which is based on American Amphibia, especially five species of *Rana*, to certain British species. All individuals were obtained in the south of England: the common frog, *Rana temporaria* L., from the Lea Valley, the common toad, *Bufo bufo* (L.), from Richmond Park, and the edible frog, *Rana esculenta* L. forma *typica*, from West Kent.

The habits of the three species differ considerably; *Rana temporaria* is moderately aquatic, but will wander some distance from water; *Bufo bufo* is aquatic only in the breeding season and is seldom to be taken in water during the summer; *Rana esculenta*, however, is the most aquatic of all the European Ranidae, being rarely found more than a few feet from the edge of a pond.

The species are not very clearly related, *Rana* being firmisternous and *Bufo* arciferous: *Rana temporaria* and *R. esculenta* are probably the most distantly related European species of their genus. All three species are very widely distributed indeed, and are very common. *R. esculenta* is local in Britain, and is usually considered to have been introduced (cf. Smith, 1939).

2. METHODS

Eggs were obtained naturally from *Bufo bufo* and *Rana esculenta*, which usually breed in the day in nature. Those of *R. temporaria*, which commonly breeds by night, were procured by squeezing ova from a female into a sperm suspension derived from the testes of a male crushed in about 10–20 c.c. water.

In the case of *R. esculenta*, the eggs used were all from one batch; some were kept at a low temperature for a few hours before being employed for the experiments.

Temperature was controlled by the use of lagged boxes, with or without an electric bulb for heating, kept in rooms with regulated temperatures. Differences of illumination were found, in a control experiment with *R. temporaria*, to be of negligible importance.

Differences of oxygenation due to temperature differences are unlikely to have been significant. Discussing *Amblystoma*, Detwiler & Copenhaver (1940) state: '...eggs can develop, and at a normal rate, with exceedingly low amounts of oxygen in the water' (p. 407).

Eggs, from about 6 to 20 in number, were kept in 100 c.c. beakers in London tap-water and examined periodically. As far as possible, they were introduced shortly before the first cleavage, but, in the other cases, they were given some hours to acclimatize before significant readings were taken. The eggs of *Rana esculenta* were introduced a little after the first cleavage.

The stages given are those of Pollister & Moore (1937) for *R. sylvatica*. In all cases where times taken to reach a given stage varied, the lowest record is given. Stages 4–6 inclusive, which cannot adequately be plotted on a graph, and stages 8 and 9, which are not easy to define, have been omitted from all tables. Stage 7 of *R. esculenta* was not studied.

As in Moore's work, the number of females used is indicated in the tables, and the data for one temperature are plotted as a straight line by varying the intervals on the abscissa (Figs. 1–3).

3. ECOLOGY AND DISTRIBUTION

R. temporaria is the most northerly of all European Anura—if not of all the Amphibia—reaching 70° N. (Boulenger, 1898), and also being recorded from 10,000 ft. The southern limit is 43° N.; and in the meridional parts of its habitat it is a mountain species replaced in the plains by *R. agilis* and its close allies.

Near London, the common frog spawns usually in March, though occasionally in February or April. Even in ponds within a few miles of each other, however, the period of maximum spawning may vary by 2 or 3 weeks in most years (Mitcham Common, Richmond Park). Eggs of this species will develop at very low temperatures—taking more than a fortnight at $3{\cdot}3 \pm 0{\cdot}2°$ C. to reach stage 10. (This is a longer period than that recorded by Hertwig, 1898.) They can tolerate at least 12 hr. at 0° C.

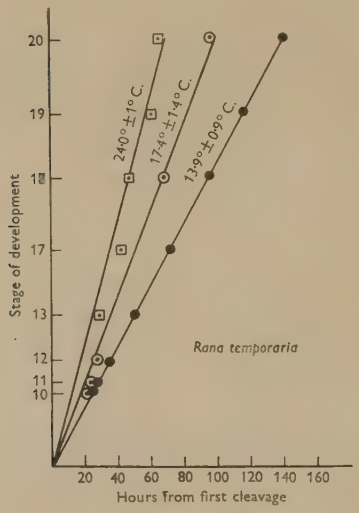

Fig. 1.

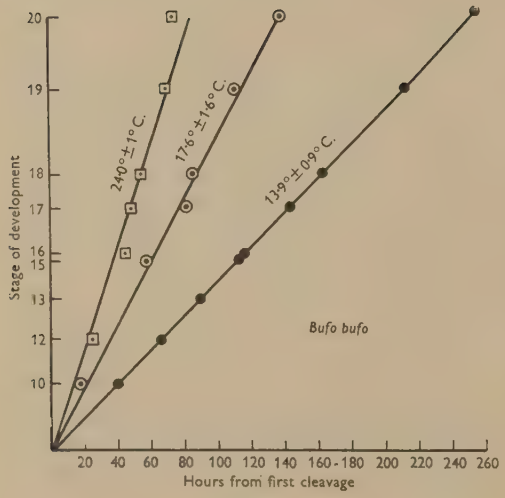

Fig. 2.

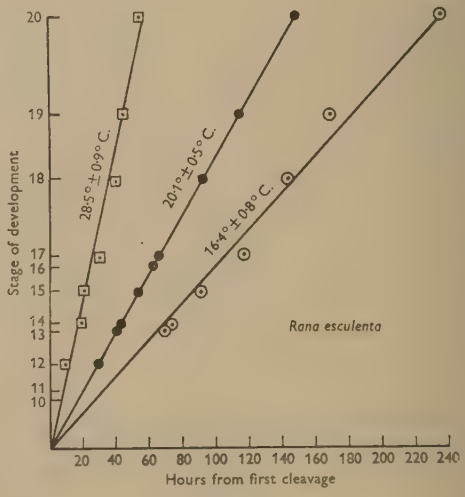

Fig. 3.

Bufo bufo is another boreal species, but less so than *Rana temporaria*. The northern and southern limits are respectively 65° N. and 34° N. The maximum elevation is 7000 ft. (Boulenger, 1898). Near London, spawning usually takes place about the first week in April.

The eggs are smaller than those of *R. temporaria* and are deposited in strings instead of batches. The embryos leave the mucilage about stage 15 or 16, instead of late in stage 20, as with *Rana*.

Some difficulty was experienced in identifying stages 14–17, because of the differences in shape from those existing in *R. sylvatica*. Stage 18 is characterized by the beginning of muscular movement.

Rana esculenta. This species extends from 59° N. (Sweden) to 28° N. (Sahara), and from Japan to

Britain. Five subspecies are recognized. Both northern and southern limits are more southerly than those of *R. temporaria* or *Bufo bufo*.

Near London, the species normally breeds rather early in May—commonly in the first spell of hot weather—but has been known to reproduce towards the end of April.

This species is more tolerant of heat but less of cold than the others, in its early stages; spawn will develop at 28·5 ± 0·9° C., while it is difficult or impossible to get eggs of *Rana temporaria* or *Bufo bufo* to survive for more than a few hours above about 24–25°. On the other hand, eggs kept at a little above freezing-point for 2 days gastrulated abnormally, the blastopore lips being unable to grow round the whole yolk plug, while those kept a little longer died before the appearance of the dorsal lip. Hertwig (1898) reports 32–33° C. as the upper limiting temperature of the embryo.

4. DISCUSSION

While the three species here studied are not closely related, the very wide distribution they all possess, and their great abundance, ensures that the data given should be strictly comparable. All extend from Western Europe to Japan, and their Asiatic limits of distribution, although different from, are in the same order as, their European ones.

We have here a close correlation between development rates and various distribution factors. As Table 4 shows, the species developing most rapidly at a temperature easily tolerated by all, also extends farthest north, is most restricted in the south, extends to the highest altitude, and, at a common latitude, breeds first. The species developing least rapidly is the opposite in all these respects, and the species intermediate in development rate is also intermediate in the other particulars.

The character of the eggs seems also to show some correlation with the other factors. Alone of European Anura, the spawn of *Rana temporaria* floats in water. This is presumably connected with the need to exploit to the utmost the early spring sunshine in order to hasten development. Furthermore, spawn is not deposited among weeds, as is the case with the other two species; this again is probably connected with the need for solar heat and the prevention of shading by water-plants.

Bufo bufo, while differing from *Rana temporaria* in these respects, yet resembles it in pigmentation. In both species, the animal (i.e. the upper) half of the egg is very dark brown in colour. (In *Bufo bufo*, and sometimes in *Rana temporaria*, the vegetable pole is also deeply pigmented, but, since that is not exposed to the sun's rays, this would not seem relevant.) This pigmented surface functions as a heat-absorber, while the very pale brown animal pole of *R. esculenta* would serve rather to reflect heat. Since the shallow water at the edge of ponds, in which *esculenta* spawns, often becomes quite warm in May or June, the problem faced by this species is rather that of preventing the eggs from getting too hot than of exploiting to the full the warmth available.

Table 1. *Time in hours taken for eggs of* Rana temporaria *to reach various stages, from time of first cleavage*

No of ♀♀ used ...	3	3	3
Temperature ...	24·0° ± 1° C.	17·4° ± 1·4° C.	13·9° ± 0·9° C.
Stage 7	4	5½	6½
10	—	21½	25
11	—	24	28
12	—	27½	34½
13	29½	—	50
14	—	—	54
15	—	52	—
16	38½	55	—
17	42½		72
18	47½	68½	96
19	61½	—	117
20	65½	97	141

Table 2. *Time in hours taken for eggs of* Bufo bufo *to reach various stages, from time of first cleavage*

No. of ♀♀ used ...	4	4	3
Temperature ...	24·0° ± 1° C.	17·6° ± 1·6° C.	13·9° ± 0·9° C.
Stage 7	5	—	—
10	—	18	40
11	21	—	—
12	25	—	66
13	—	—	90
14	—	44½	—
15	—	58	114
16	45	—	118
17	49	82	143
18	55	86	163
19	70	111	216
20	74	139	257

Table 3. *Time in hours taken for eggs of* Rana esculenta *forma* typica *Blgr. to reach various stages, from time of first cleavage*

No. of ♀♀ used ...	1*	1*	1*	1
Temperature ...	28·5° ± 0·9° C.	24·2° ± 1·4° C.	20·1° ± 0·5° C.	16·4° ± 0·8° C.
Stage 10	—	6	18	—
11	—	—	21	—
12	10	—	30	—
13	—	19	41	70
14	20	—	44	75
15	22	—	55	91
16	—	31	63	—
17	31	33	67	119
18	—	46	93	145
19	45	55	115	170
20	55	69	147	235

* Compare text.

Table 4. *Comparison of certain data for three Anura*

Species	*Rana temporaria*	*Bufo bufo*	*Rana esculenta*
Normal breeding month near London	March	April	May
Most northerly record	70° N.	65° N.	59° N.
Most southerly record	43° N.	34° N.	28° N.
Maximum elevation	10,000 ft.	7000 ft.	3500 ft.
Interval between stages 3 and 20 at 17·6° ± 1·6° C.	97 hr.	139 hr.	170 hr.*

* By interpolation.

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ANNUAL TRENDS IN A NATURAL POPULATION OF *THRIPS IMAGINIS* (THYSANOPTERA)

By the late J. DAVIDSON and H. G. ANDREWARTHA*
From the Waite Agricultural Research Institute, University of Adelaide

(With 5 Figures in the Text)

1. INTRODUCTION

The apple blossom thrips (*Thrips imaginis* Bagnall) is widely distributed in Australia, where it is an indigenous species. The biology of *T. imaginis* was investigated a few years ago by a team of workers consisting of officers of the Council for Scientific and Industrial Research and the Waite Institute. A summary of the information established by these workers was given by Davidson (1936). The eggs are usually laid in the tissues of flowers. Pollen is essential for reproduction as practically no eggs were laid by females from whose diet pollen had been excluded (Andrewartha, 1935). Nymphs and adults may be found feeding in the flowers of a large variety of plants. The nymphs usually leave the flowers to pupate in the soil or debris around the plant (Evans, 1932). In the Adelaide area the species is active throughout the year, but the population attains its greatest density during spring and early summer (September to December). The density varies greatly from year to year.

During the years 1932–8 the number of *T. imaginis* in roses in the garden at the Waite Institute was recorded throughout each year. Since 1938 samples have been taken only during the spring and early summer (September to December). There is thus a continuous record of the numbers of *T. imaginis* in roses throughout the year for 82 consecutive months; and records for the numbers present during spring and early summer are available for 14 years. This paper discusses in general terms the fluctuations and the annual trends in the density of the population as revealed by a study of the records for the 81 consecutive months. Later it is hoped to analyse more particularly the association between the numbers of thrips and the weather; and for this the full 14 years' records will be used.

* The late Prof. J. Davidson was the leader of a team of workers who spent several years studying the biology of *Thrips imaginis*. The present series of population counts was begun by J. W. Evans in April 1932: on his departure from South Australia they were continued by H. G. Andrewartha. Prof. Davidson was working on these data with the object of measuring the association between the density of the thrips population and the weather, but unfortunately the work was still unfinished when he died in August 1945. The work was taken over and brought forward to its present condition by H. G. Andrewartha.

2. METHOD OF SAMPLING

Roses were selected for sampling because they are a favourite host of *T. imaginis*, and also because some roses may be found on the bushes throughout the year. During most of the year, usually for about 8 months (October to May) flowers were collected from a hedge of 'Cecil Brunner' roses; but during the remainder of the year it was often necessary to substitute another variety known locally as 'Monthly Rose'. The two hedges are growing within a few chains of each other and there is no evidence that one variety attracts more thrips into the flowers than the other.

The method of sampling was described by Evans (1933*a*). Each day about 9 a.m. 20 roses were collected and placed in a box with a tight-fitting lid. They were taken to the laboratory and the number of adult *T. imaginis* in the sample was recorded. So far as possible, the roses were selected at a uniform stage of development, i.e. when the flower was fully open and just before the petals had begun to fall. This stage may occur 1–4 days (depending on the weather) after the 'open-bud' stage at which the roses first become attractive to the thrips. During the 82 months that records were made samples were taken on 1773 days (see Table 1).

Only one sample of 20 roses was taken each day and the number of thrips was recorded for the sample and not for individual roses, so the data did not permit of an estimate of the sampling variance. But a separate experiment was done to measure the sampling variance on 8 different days between 13 October and 4 December 1944. On these days 40 'Cecil Brunner' roses were collected as usual at random from the hedge, but on this occasion the number of thrips present in each rose was recorded separately. The roses were divided into two groups of 20 each by numbering them at random 1–40, and then placing the odd numbers in one sample and the evens in the other. The results are set out in Table 2.

Table 1. *Number of sampling days each month*

Year	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Total
1932–3	21	26	25	15	15	21	25	26	21	24	24	27	270
1933–4	20	27	22	15	16	19	25	26	20	25	24	25	264
1934–5	22	27	26	26	16	24	24	25	18	23	24	25	280
1935–6	19	25	18	15	25	25	26	27	26	25	24	17	272
1936–7	25	26	24	16	22	22	24	22	14	21	22	23	261
1937–8	21	14	7	11	12	20	26	26	21	23	24	27	232
1938	21	26	13	25	16	22	26	25	20	—	—	—	194
Total	149	171	135	123	122	153	176	177	140	141	142	144	1773

Table 2. *Number of thrips in parallel samples of 20 roses*

Based on samples of 20 roses

Date	Arithmetic means		Geometric means		Geometric mean based on 40 roses
	'Odds'	'Evens'	'Odds'	'Evens'	
13 Oct.	26·8 ± 3·42	40·6 ± 5·57	22·4	33·8	27·5
19 Oct.	20·6 ± 3·77	24·3 ± 5·59	13·8	13·9	13·9
23 Oct.	60·9 ± 10·47	63·6 ± 9·89	41·7	48·2	44·8
25 Oct.	57·7 ± 9·06	63·9 ± 11·15	41·5	39·6	40·6
30 Oct.	83·6 ± 9·78	85·9 ± 13·00	62·8	69·0	65·8
1 Nov.	104·1 ± 20·36	106·1 ± 14·84	77·4	82·0	79·6
3 Nov.	137·5 ± 15·61	110·3 ± 9·53	115·1	103·0	108·9
4 Dec.	68·0 ± 5·21	67·7 ± 7·76	63·8	57·3	60·4
Mean	69·9	70·3	—	—	—

S.E. (in logarithmic scale) for mean of 20 for 'odds', 0·078; for 'evens', 0·081; for mean of 40, 0·056;

The table shows the standard error for each mean of 20 roses (using 19, i.e. $n-1$, as divisor for the sums of squares), as well as the geometric means for the parallel samples of 20 roses and for the larger samples of 40. On inspection of the means and standard errors of the 'odds' and 'evens' it is seen that the means and their variances are similar for each of the eight pairs of samples taken on the same day: the correlation coefficient for the eight pairs of means is 0·92 and the regression coefficient of 'odds' on 'evens' is 0·75. On the other hand, the variances within each group of 8 days are manifestly not homogeneous. Accordingly the data were transformed to logarithms so that the variances might be pooled. The standard errors for the means of 20 and 40 in the transformed scale are given under the table. Significant differences ($P=0{\cdot}05$) between pairs of means in the transformed scale are 0·22 for 'odds', 0·23 for 'evens' and 0·16 for means of 40. The estimates of the number of thrips in the roses were more precise with the larger samples. For example, with the samples of 20 there was no significant difference between the samples collected on 23 and 25 October and that collected on 30 October, but with the samples of 40 the difference between the last one and the first two in this group was clearly established. Although it might have been desirable to have greater precision than was given by the samples of 20 roses it was not practicable to work with larger samples, and it is considered that the data provide a useful estimate of the numbers of thrips in the roses on any one day.

In this and a later paper, it is proposed to consider the changes in the numbers of thrips in roses from day to day in relation to: (*a*) the natural growth of the population; (*b*) the influence of the weather throughout the year on the growth of the population; and (*c*) the influence of the weather at about the time that the sample was taken on the activity of the adults in seeking out flowers. It is therefore necessary to consider, in relation to sampling methods, what else may influence the daily counts of thrips in the roses.

At certain times during the year the bushes of one variety of rose may be densely covered with flowers while the other variety may carry only a few flowers. On such occasions it was usual to find more thrips in the roses from the hedge where there was a lot of flowers than in those from the hedge with only a few flowers. From this it may be inferred that the number of thrips found in the roses may have been influenced by the density of the roses on the hedge when the sample was taken. But as there was usually an abundance of roses during the spring and early

summer (October–December) this source of error may not have been important during this period. There is some evidence that thrips come and go from flowers more or less in waves and in so far as this may be due to inherent gregariousness in the species, it contributes variability which is not readily measurable. And finally it must be recognized that the sample of 20 roses may not represent a constant proportion of all the niches available to *T. imaginis* in the garden from day to day. None of the several sources of error discussed in this paragraph has been measured, but it is considered that they may be quite small compared with the big fluctuations in the numbers of thrips which have been observed.

3. DAILY RECORDS OF THE NUMBERS OF *THRIPS IMAGINIS* IN ROSES THROUGHOUT A COMPLETE YEAR

A striking feature of the daily records, as illustrated in Fig. 1, are the large and abrupt daily fluctuations in the numbers of thrips found in the flowers. This was not peculiar to the period shown in the figure, but was common to all the years that records were kept. The

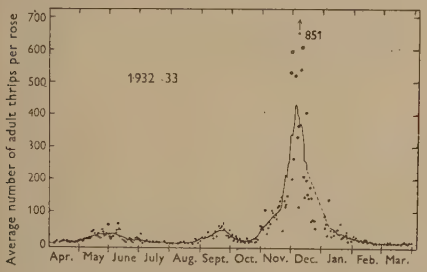

Fig. 1. Daily records of the average number of adult *Thrips imaginis* per rose for 12 consecutive months, from April 1932 to March 1933. The curve represents a 15-day moving average of the daily counts.

daily fluctuations were not quite erratic, but rather tended to follow short cycles with a period of a week or less. It is considered that they may be related to the influence of the weather on the 'activity' of thrips at, or shortly before, the time the sample was taken. This matter will be discussed more fully in a later paper. The fluctuations became more pronounced during the spring and early summer when the density of the population was great, but they were also quite marked at other periods of the year, and are apparently inherent in the behaviour of *T. imaginis* in this environment.

The females do not lay eggs in batches, but lay several eggs each day continuously throughout their adult life; and an adult may live for several months at the temperatures experienced during the spring (Andrewartha, 1935). Although there is a tendency for the proportion of adults in the population to be relatively higher at the end of the winter, the population at any time includes individuals of various stages and ages; the generation effect is therefore not likely to be pronounced (Davidson, 1944*a*). Consequently, the growth and decline of the population may be represented by a smooth curve.

The curve in Fig. 1 has been drawn through a 15-day moving average calculated from the individual daily counts, which are also shown in the figure. The numbers were at their lowest during late winter (July–August) when temperature was low and flowers were scarce, and they were also low during late summer (February–March) when flowers were again scarce and heat and dryness reduced the favourableness of the environment. There was a small increase in the late autumn (May–June) which may be associated with the early 'break' of the season in 1932; good rains fell in March–April and maintained adequate soil moisture, while temperature was still adequate for development of *T. imaginis* and its host plants. The population grew rapidly during the spring and early summer (September–December) which was the only period of the year when there was an abundance of host flowers, and the temperature and soil moisture were adequate for rapid multiplication. The temporary decline in numbers during October was associated with an unusually cold wet period and a temporary shortage of roses on the bushes at this time (Evans, 1933*b*). There was an abrupt decline in numbers during December–January associated with the disappearance of the spring flowers and the onset of the dry season.

In the Adelaide area rain associated with moderate temperature during the winter provides a 'growing season' of about 7 months (Trumble, 1937). The rest of the year is hot and dry. The march of the seasons is fairly regular, but there are relatively wide variations in the date of the 'break' of the season and the amount of rain which falls during the autumn, and also in the date of onset of the dry season. This variability is reflected in a corresponding variability in the growth of the population of *T. imaginis* each year.

4. FLUCTUATIONS IN THE GROWTH OF THE POPULATION IN THE SPRING

The date in the spring when the numbers began to show a progressive increase differed from year to year; so did the date on which the numbers reached a maximum (Fig. 2). The curves were drawn through 15-day moving averages derived from the original counts. The moving average smooths out the day to day fluctuations and short-term oscillations, thereby bringing out more clearly the secular trend of the

population. Moving averages for 5-day and 10-day intervals were also tried, but it was found that the short-term oscillations were not removed sufficiently; and the 15-day moving average was chosen because the short-term oscillations seemed to be adequately smoothed out without unduly eliminating the longer term oscillations which are more properly related to the secular trend of the population (Kendall, 1941).

The greatest mean number of *T. imaginis* for a 15-day period during the 7 years was 746 on 20 November 1938, this being the central day of the 15-day period 13–27 November. The lowest mean peak density occurred in 1934 with 82 on 8 December: the mean peak density for 7 years was 309. Corresponding figures based on actual counts instead of on 15-day moving averages are given in Table 4.

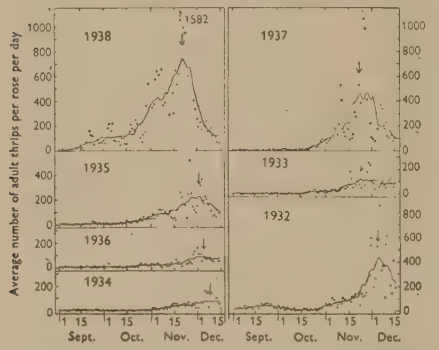

Fig. 2. Growth and decline of the thrips population during spring and summer for 7 consecutive years 1932–8. The curves represent 15-day moving averages of the daily records which are shown as dots in the diagram. The arrow indicates the maximum of each curve.

From Table 4 and Fig. 2, it is clear that there was an association between earliness of peak and height of peak; that is, the maximum of the curve was greater for those years when the summer decline in numbers began early. From the data in columns 4 and 5 of Table 4 the correlation between days and thrips (at the maximum of the curve) is $-0{\cdot}82$ and the regression of thrips on days is -31, indicating that, on the average, the maximum reached was 31 less for every day that the date of onset of the summer decline was postponed. The explanation for this paradox may be sought in the influence of the weather on the growth of the thrips population in the spring, more particularly the indirect effect of the weather influencing the plants which are hosts for *T. imaginis*.

In the Adelaide area the spring is the one season of the year when the influences of temperature, moisture and food is likely to be most favourable for the multiplication of *T. imaginis*. When an abundance of food is available early in the spring the usual increase in numbers may be expected to begin sooner and proceed more rapidly, giving rise, on these occasions, to a relatively dense population relatively early in the spring.

During the 15 years between 1932 and 1946 a number of the plants which serve as hosts for *T. imaginis* came into full-bloom much earlier in the spring in some years than in others; and usually there was a greater abundance of flowers in those years when the blossoming period began early. In general, an early and profuse blossoming occurred in those years when the wet season began early in the autumn and thus allowed the plants to make adequate vegetative growth before the low temperatures of

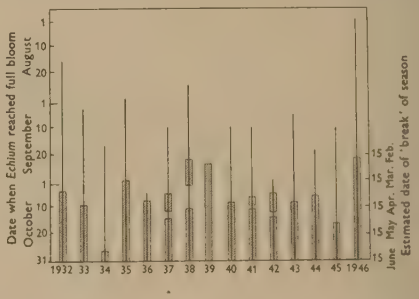

Fig. 3. The tops of the solid narrow columns indicate the date when *Echium plantagineum* was first observed in full bloom. The height of the narrow columns indicates the duration of the flowering period up to 31 October each year. The tops of the broad hatched columns indicate the date when the 'growing season' was estimated to have commenced each year.

winter had set in. This is illustrated for one species (*Echium plantagineum*) in Fig. 3. The thin solid columns indicate the number of days prior to 31 October when the species was first observed in full bloom; and the broader hatched columns indicate the number of days prior to 15 June when the 'break' of the season was estimated to have occurred each year. The estimate was made by the method already described by Trumble (1937). The records for rainfall and evaporation at the Waite Institute were used. Starting with the first substantial fall of rain in the autumn a progressive total of rainfall was calculated by adding the daily rainfall and subtracting one-third of the daily evaporation. The broad-hatched columns in the figure represent the period during which this progressive total remained above zero each year. The association between early autumn rains and the early flowering of *E. plantagineum* in the spring is apparent.

No record was kept of the decline of the blossoming period, but this may be expected to end sooner and more abruptly in those years when the plants had made adequate vegetative growth before the winter, since the flowering period of the plant is related to its earlier vegetative growth. Also, on the average, the date of onset of the seasonal summer drought may be expected to be earlier in those years when the autumn 'break' of the season occurred early, since Cornish (1936) showed that the duration of wet season tended to be constant, but there was a definite oscillation with an amplitude of about 30 days in the incidence of the winter rains.

particularly noticeable in 1932, 1937 and 1938. In certain years, as in 1938, there were well-defined secondary trends in the growth of the population so that the trend of the data could not be faithfully represented by a single logistic curve. The appearance of the secondary curves varied from year to year and they were not apparent in some years, as in 1936. They may be related to the appearance in the roses of adults of the second and third spring generation, and to the influence of the prevailing weather on the rate of multiplication of the insects and the movements of the adults (Davidson, 1944*a*). But these differences in detail do not conceal the general similarity in the

Table 3. *Average number of thrips per rose per day for each month, based on counts from 20 roses per day for 1773 days*

Month	1932/3	1933/4	1934/5	1935/6	1936/7	1937/8	1938	Mean
Apr.	4·5	2·4	6·1	2·6	3·3	2·0	3·5	3·5
May	23·4	3·9	14·4	6·2	8·1	3·0	11·6	10·1
June	17·8	5·3	26·9	16·5	12·9	4·8	5·6	12·8
July	4·4	5·5	6·7	0·8	9·1	2·5	7·9	5·3
Aug.	3·3	1·7	3·7	1·7	1·8	1·7	5·4	2·8
Sept.	34·0	2·8	5·9	5·5	4·3	4·6	50·7	15·4
Oct.	13·8	10·1	1·6	21·9	11·2	24·4	157·8	34·4
Nov.	133·7	78·3	36·0	133·5	41·1	310·4	574·6	186·8
Dec.	267·4	71·3	76·3	136·6	69·0	127·4	137·6	126·5
Jan.	37·8	15·5	14·5	15·9	5·9	15·6	—	17·5
Feb.	9·8	5·1	7·8	5·7	2·9	6·2	—	6·3
Mar.	2·8	7·3	3·7	6·3	3·7	4·0	—	4·6

5. AVERAGE TREND IN THE NUMBERS OF THRIPS IN ROSES

It is not practicable to publish the individual counts for the 1773 days when samples were collected because of the amount of space required. The data have been combined to show the average number of thrips per rose per day for each month (see Table 3, column 9).

The number of sampling days in each month was given in Table 1. It is apparent that the numbers of thrips were usually at their lowest during August; the population grew rapidly during September–November and declined during December–January; numbers remained low for the remainder of the year except for a small increase during May–June. In some years the increase in numbers during May–June was not observed; but in all other respects the same trends in the density of the population were repeated (with differences in detail) each year.

The trend of the growth of the population in the spring (Fig. 2) can be adequately represented by a logistic function (Davidson, 1944*a*); more particularly by a portion of the logistic curve, since in most years the decline set in somewhat abruptly before the population had achieved the potential density indicated by the earlier stages of its growth. This was

trend of the population during the spring of each of the 7 years.

Accordingly it was possible to combine the 7 years to obtain a set of mean values which represented the average trend of the population during the spring for 7 years. But before combining them the curves were moved along the date axis to bring the peaks under each other: it seemed wiser to choose this natural end-point to the growth curve rather than some arbitrary date on the calendar. The date on which the 15-day moving average reached a maximum varied from 20 November in 1938 to 8 December in 1934. The mean date for the peak was 30 November $\pm$ 2·6 days (Table 4).

Accordingly, each of the seven graphs on Fig. 2 was moved backwards or forwards the appropriate number of days so as to bring the day having the maximum population under 30 November. For example, the points on the chart for 1932 were moved back 4 days so that the value for the peak day (433 thrips on 4 December) came under 30 November; the curve for 1938 was moved forward 10 days to bring 20 November (746 thrips) under 30 November; the points for the remaining years were also set forward or back the appropriate number of days. When the daily values for each year had been adjusted in this way, the average value for 7 years was obtained

Table 4. *Maximum number of thrips per rose for each year and the date on which the maximum occurred*

Year	Based on daily counts		Based on 15-day moving average	
	No. of thrips	Date	No. of thrips	Date
1932	851	5 Dec.	433	4 Dec.
1933	256	28 Nov.	116	1 Dec.
1934	163	5 Dec.	82	8 Dec.
1935	362 (522)*	3 Dec. (23 Nov.)	228	1 Dec.
1936	157	30 Nov.	89	4 Dec.
1937	1122	24 Nov.	469	22 Nov.
1938	1582	19 Nov.	746	20 Nov.
Mean	642 ±209·9	29 Nov. ±2 days	309 −94·5	30 Nov. ±2·6 days

* An isolated record not associated with the period of greatest abundance.

for each of the 106 days between 1 September and 15 December.

These values have been plotted in Fig. 4. The 91 values from 1 September to 30 November were fitted to a logistic function of the form $Y = d + \frac{K}{1+e^{a-bx}}$, where Y represents the average number of thrips per rose on any given date x, d is the height of the lower asymptote, K the height of the upper asymptote and a and b are constants calculated from the data. The particular equation calculated from this set of data was

$$Y = 7 + \frac{640}{1+e^{6\cdot49655-0\cdot06765x}}.$$

The curve shown in Fig. 4A was calculated from this equation. The root mean square deviations of the 91 observed values from the calculated curve is 7·41. This may not be the best-fitting logistic curve but it serves to define the trend of the data.

The formula for the logistic function given above implies that there is a linear relationship between x and the logarithm of $\frac{K-y+d}{y-d}$ (Davidson, 1944*b*). The points in Fig. 5A follow a sinuous course about the calculated straight line indicating that there are secondary trends within the course of the average daily values plotted in Fig. 4A.

Accordingly the 91 values were divided into three groups as follows:

(*a*) 1 September to 9 October 39 days;
(*b*) 10 October to 11 November 33 days;
(*c*) 12 November to 30 November 19 days.

The data for each period were fitted to the logistic formulae giving the following equations:

$$(a)\quad Y = 4 + \frac{28\cdot7}{1+e^{2\cdot2884-0\cdot06218x}};$$

$$(b)\quad Y = 16 + \frac{302}{1+e^{9\cdot0499-0\cdot1171x}};$$

$$(c)\quad Y = 126 + \frac{223}{1+e^{23\cdot096-0\cdot2685x}}.$$

The three curves shown in Fig. 4B correspond to these equations. The root mean square of the deviations of the observed points from the calculated curves are (*a*) 0·790, (*b*) 1·455, (*c*) 5·779. The appropriate values for $\log \frac{K-y+d}{y-d}$ are shown in Fig. 5B. The observed points appear to be distributed more at random about the calculated straight lines than was the case with Fig. 5A. The curves in Fig. 4B may not

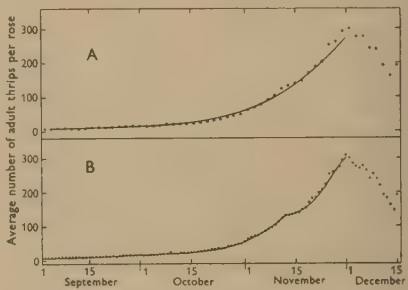

Fig. 4A. Part of a logistic curve illustrating the mean trend of the thrips population during spring and early summer for 7 years 1932–8. B. A composite curve made up of parts of three logistic curves, fitted to the same data. Formulae for these curves are given in the text. The observed points were obtained by taking 15-day moving averages of the daily counts, adjusting these to the 'peak' date and taking the mean for 7 years.

be the best logistic curves that could be fitted to this data, but from an inspection of Fig. 5 and from the lower values for the root mean square it may be inferred that the composite curve of Fig. 4B represents the trend of the population somewhat more faithfully than the simpler curve of Fig. 4A. By making the appropriate calculations it is possible to obtain the best-fitting logistic curve for any set of data (Birch, 1944); but the calculations are laborious and seem hardly appropriate in this case having regard to the relatively small departures of the observed from the calculated values for the curves that have been chosen.

These departures are relatively quite small compared with the variability of the data from which the curves have been calculated. For example, the mean for the 7 'peak' days was 642 ± 209 (Table 4). A further example is provided by the data in Table 5. The last column was calculated from the data used to calculate the curves in Fig. 4, i.e. from the data after

the curves had been moved to make the peaks coincide; the third column was calculated from the data used to plot the curves in Fig. 2; and the second column was calculated from the original counts.

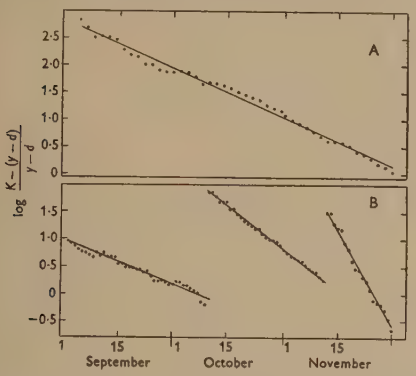

Fig. 5 A. Showing the individual values of $\log \frac{K-y+d}{y-d}$ for the data of Fig. 4A. B. Showing the individual values of $\log \frac{K-y+d}{y-d}$ for the data of Fig. 4B.

Table 5. *Mean number of thrips per rose and the standard error of the mean for selected days, for 7 years*

A, using original daily counts; B, using 15-day means; C, using 15-day means adjusted so that maxima coincide

Date	A	B	C
30 Sept.	21·3 ± 10·8	23·4 ± 10·4	15·5 ± 8·8
30 Oct.	59·6 ± 21·1	82·3 ± 43·8	49·4 ± 15·8
30 Nov.	200·0 ± 70·8	229·7 ± 57·0	309·0 ± 94·5

The relatively high values for standard error of the means indicate the high variability in the density of the population during spring for the 7 years. Since the density of the thrips population may be influenced by several components of the weather it may be expected that the variability of the thrips population would exceed the variability of any one component of the weather. It is usually considered that some 30 years' records may be required to give a reliable estimate of the mean monthly rainfall in the Adelaide area. Considerably more than 7 years' records of thrips numbers may be required to give an adequate estimate of the mean density or mean trend of the density of the population of *Thrips imaginis*: perhaps 40 or 50 years' records would be sufficient.

6. SUMMARY

During 1932–8 the numbers of adult *Thrips imaginis* in roses were counted on 1773 days, giving a continuous record for the density of the population during 81 successive months. The total variability of the 1773 daily records may be considered to have three components due respectively to (*a*) the natural growth of the population; (*b*) the influence of weather, about the time the sample was taken, on the activity of the thrips in seeking out flowers; (*c*) the influence of the weather throughout the year on the rate of multiplication of the insects. The same trend of population tends to be repeated each year, and it is possible to represent the average trend for 7 years by a smooth curve. The average trend during the period 1 September to 30 November (when the population is increasing rapidly) may be represented by part of a curve fitted to the logistic formula $Y=d+\frac{K}{1+e^{a-bx}}$. The sources of variability referred to (*b*) and (*c*) above have been discussed in general terms in this paper, and it is hoped to deal with them more particularly in a later paper.

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THE INFLUENCE OF RAINFALL, EVAPORATION AND ATMOSPHERIC TEMPERATURE ON FLUCTUATIONS IN THE SIZE OF A NATURAL POPULATION OF *THRIPS IMAGINIS* (THYSANOPTERA)

By the late J. DAVIDSON and H. G. ANDREWARTHA*
From the Waite Agricultural Research Institute, University of Adelaide

(With 5 Figures in the Text)

1. INTRODUCTION

The apple-blossom thrips (*Thrips imaginis* Bagnall) is indigenous to southern Australia. Several times during the past 40 years mass outbreaks of the species have caused widespread damage to apple blossom in West Australia, South Australia, Victoria and New South Wales. During an outbreak large numbers of the insects leave the flowers of weeds and other plants where they have been breeding and enter the flowers and flower-buds of the apple; the movement may be more marked during warm dry days. Mass outbreaks usually occur simultaneously over a remarkably wide area. For example, in 1926 and again in 1931 the plague was widespread in all apple-growing areas of South Australia, Victoria, and also parts of New South Wales (Evans, 1932).

These areas are separated by almost a thousand miles, and it is difficult to imagine any set of causes other than long-term fluctuations in the weather which might operate simultaneously over such a wide area. The weather may be associated with the growth and decline of the thrips population directly by the influence of temperature and soil moisture on the rate of development and the survival rate of the insects, and indirectly by the influence of the same factors on the development of the plants which are hosts for *T. imaginis*.

There is a regular annual cycle in the growth and decline of the population, but the annual variation, both in the maximum size attained by the population and the date when the maximum is reached is considerable. For example, the average for November 1934 was 36 compared with 575 for November 1938 (Davidson & Andrewartha, 1948). Since it was considered that fluctuations in the physical environment of the insects may be important in causing fluctuations in the thrips population the present study was directed towards measuring the degree of association between the numbers of thrips present in the roses during spring and early summer and those components of the weather which were considered to be causally related to the size of the population. The method of partial regression has been used; in choosing the independent variates we have been guided by a knowledge of the biology of *T. imaginis* and of the climate of the Adelaide area.

The biology of *T. imaginis* was studied by a team of workers under the direction of the late Prof. J. Davidson and the results of their work were summarized by him (Davidson, 1936). The climate of the area has been extensively studied by a school of workers at the Waite Institute, and summaries of their published work have appeared from time to time in the Report of the Waite Institute.

2. MATERIAL

For 14 years during the period 1932–46 daily counts have been made of the numbers of adult *T. imaginis* in roses in the garden at the Waite Institute; during 1944 records were not kept owing to pressure of other work. During the 7 years 1932–8 a sample of 20 roses was taken daily throughout the year; from 1939 onwards a sample of 10 roses was taken daily during the spring and early summer (September–December); this is the season when the population attains its maximum size each year. Usually samples were not taken on Sundays nor on holidays; the number of sampling days for each of the months from September to December for the 14 years are shown in Table 1: altogether 1252 daily records were taken. The method of sampling was described and discussed elsewhere (Davidson & Andrewartha, 1948). The roses used for sampling were attractive to the adult thrips but were not favourable for the development of the immature stages. They served as a 'trap' which gave a satisfactory indication of the density of the population in the area.

* The late Prof. J. Davidson was the leader of a team of workers who spent several years studying the biology of *T. imaginis*. The present series of population counts was begun by J. W. Evans in April 1932: after his departure from South Australia they were continued by G. H. Andrewartha. Prof. Davidson was working on the data with the object of measuring the association between the density of the thrips population and the weather, but unfortunately the work was still unfinished when he died in August 1945. The work was taken over and brought forward to its present condition by H. G. Andrewartha.

The rainfall, evaporation and atmospheric temperature were measured at the meteorological station situated at the Waite Institute, a few chains away from the garden where the roses were growing. The records were made on standard instruments described in the Australian Meteorological Observers' Handbook.

Table 1. *The number of sampling days each month for 14 years*

Month	1932	1933	1934	1935	1936	1937	1938	1939	1940	1941	1942	1943	1945	1946	Total
Sept.	21	19	24	25	22	20	22	25	17	25	18	15	19	15	287
Oct.	25	25	24	26	24	26	26	24	27	25	27	25	26	26	356
Nov.	26	26	25	27	22	26	25	26	24	24	24	26	23	24	348
Dec.	21	20	18	26	14	21	20	13	13	24	17	21	15	18	261
Total	93	90	91	104	82	93	93	88	81	98	86	87	83	83	1252

3. METHOD

The total variability of the 1252 daily records may conveniently be ascribed to four components. Each year the numbers in the roses start from a low level at the end of the winter; they increase usually rapidly and continuously until they reach a maximum about the end of November and then decline again (Davidson & Andrewartha, 1948). The growth of the population with time within each year may be regarded as one component of the total variability of the daily counts. The numbers of thrips present at the end of the winter, the rate at which the numbers increase and the size of the maximum attained, may all vary from year to year; thus the second component of total variability may be specified as variation in the growth of the population from one year to another. The number of thrips recorded in the roses may be taken as one criterion of the numbers present in the garden: but this estimate of the population will be more variable than the true numbers of the thrips in the garden to the extent that the mean number of thrips per rose in the daily sample is not a constant proportion of the total number of thrips in the garden. A number of causes may operate to vary this proportion: for example, the thrips may be more active in seeking out the roses during a warm dry day than during a cold wet one. It is convenient to specify the third component of variability as the variation due to the variable 'activity' of the insects in seeking out the roses. Finally there is the residual variability which may be considered as being random with respect to the three components which have been selected for special study.

The method consisted essentially of studying the second and third components one at a time, after having first eliminated as much as was practicable of the variance associated with the other components. Before describing the method more particularly, it is appropriate to consider (without at this stage giving detailed consideration to the nature of the 'cause') the sort of relationship which may exist between the '*cause*' (various elements in the weather) and the '*effect*' (fluctuations in the numbers of thrips).

Experience indicates that the thrips numbers are not likely to change by a constant quantity for each increment in the causal agent but rather are they likely to change by a constant proportion. This may be expressed in symbols: the expected relationship would not be $Y=kx$, but would be of the form $Y=ka^x$; or, when several causes may be operating together, $Y=k\times a_1^{x_1}\times a_2^{x_2}\times a_3^{x_3}\ldots$. This expression assumes the form of the partial regression equation when logarithms are written in place of the original quantities:

$$\log Y=\log k+x_1\log a_1+x_2\log a_2\ldots.$$

In this expression $\log k$ is the logarithm of the geometric mean of y; and $\log a_1$, $\log a_2$ are the partial regression coefficients of y on x_1 and x_2 when the logarithm of y is used in the place of the original value of y.

Accordingly, all records of the daily counts of thrips per rose were converted to logarithms. It is fortunate that in this instance the logarithms of the thrips counts were distributed very nearly normally, whereas the distribution of the original counts was strongly skew (see Fig. 1). Thus the transformation to logarithms, which was made in the first instance for the practical purpose of satisfying the expectation that independent and dependent variates would be related in a particular way, also transforms the data to a form that is appropriate for statistical treatment.

The method of partial regression as described by Fisher (1941, p. 149) is admirably suited for the treatment of data of this sort. The use of the 'c' multipliers makes it practicable to include a number of independent variates and with little labour to discard successively the less important of them. Furthermore, very little extra labour is involved in using successively a number of different estimates of the dependent variate with the same series of independent variates. In this way the mutual relationships of the data may be explored with precision and with remarkably little extra labour.

There are two qualities of the partial regression coefficient which are worthy of emphasis in relation to the present study. The partial regression coefficient expresses the degree of association between its independent variate and the dependent variate when all

other terms *included in the regression* are held at their means. For example, when the equation includes two terms which are not only closely associated in the same direction, with each other, but also with the dependent variate, the regression measures the degree of association which each has with the dependent variate independent of the influence of the other; but neither may have an appreciable effect independent of the influence of the other; and the total effect measured in the regression equation may not be large. The correct procedure is to discard one of them and leave the other to measure the influence of both; for the regression coefficient always includes in itself not

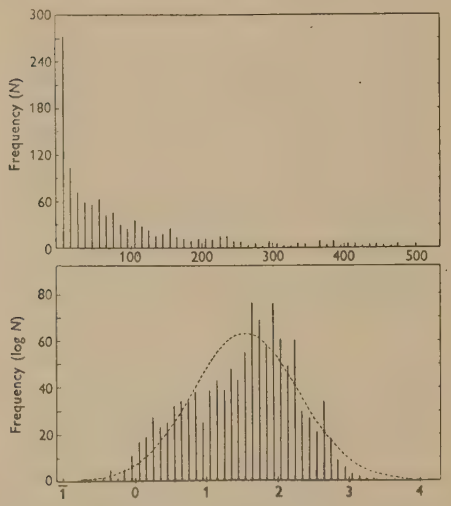

Fig. 1. The distribution of the daily counts of thrips per rose (above); and the distribution of the logarithms of the daily counts (below). The broken line represents the normal curve having the same mean and standard deviation as the observed data.

only a measure of the degree of association of the dependent variate with the particular independent variate but also of all terms *not included in the regression* which are associated with the independent variate.

The regression equation measures only association. Causality requires to be inferred from independent sources. In the present instance an adequate knowledge of the biology of *T. imaginis* has led to the selection of independent variates which have accounted for a substantial part of the total variance. In his pioneer work in this field Williams was dealing with groups of species, and the same degree of detail in postulating causal relationships was not always practicable with his material (Williams, 1940). Also with Williams's data the greater part of the total variance was due to variable activity of the insects in seeking out the trap: and relatively little of the total variance could be attributed to fluctuations in the abundance of the insects in the area. With the present paper the reverse is the case.

4. DAILY FLUCTUATIONS IN THE NUMBER OF THRIPS IN THE ROSES

In any one year during the period when the population is increasing rapidly in size the variability in the daily counts may be ascribed to: (*a*) natural increase with time in the number of thrips in the garden; (*b*) variable 'activity' of the thrips in seeking out the flowers; (*c*) residual or random variation.

(*a*) *The elimination of variability due to trend with time*

There are theoretical grounds for expecting the trend of the population with time to approximate to a logistic curve (Davidson, 1944; Davidson & Andrewartha, 1948). But the logistic formula is not easy to handle with all types of data, and has certain other disadvantages; so, for the present purpose, polynomial curves were used to eliminate trend with time. A curve of predetermined degree was calculated for the 60 days which preceded the day when the population attained its maximum. The period 60 days was chosen because this gave a satisfactorily long run of observations and for most years the population increased continuously and rapidly for a period of at least 60 days before it attained its maximum. The date of the 'peak' of the population was determined by the method described elsewhere (Davidson & Andrewartha, 1948): 15-day progressive means were calculated from the logarithms of the daily counts of thrips per rose and the maximum of the curve was considered to occur on the central day of the 15-day period having the highest mean value.

In order to avoid the labour of calculating polynomial coefficients from the full 60 daily records the data were grouped: 3-day intervals were chosen giving 20 groups. A curve of the third degree in x (days) was fitted to the means of the 20 groups, using Fisher's method of orthogonal polynomials. The trend of the data with time (i.e. the regression of log thrips on days) varied considerably from year to year. The figures in Table 2 indicate the extent and direction of this variation: the table sets out the regression coefficients for each of the 14 years. The table also shows that the residual variance was relatively high for some years. For example, a fourth term was fitted to the regression for 1932; E' was found to equal $0{\cdot}1257 \times 10^{-3}$, and was significant at the 1 % level of probability ($t = 4{\cdot}056$). Nevertheless, it was considered that the regressions for most years

Table 2. *Showing the regression coefficients for log thrips on time for the 60 days preceding the peak for each of 14 years. The residual variance (s^2) is also shown*

The data for $n=60$ were derived from the values for $n=20$ (see below)

	$n=20$					$n=60$			
Year	A'	$B' \times 10^3$	$C' \times 10^3$	$D' \times 10^3$	$s^2 \times 10^3$	$B' \times 10^3$	$C' \times 10^3$	$D' \times 10^3$	No. of observations during 60-day period
1932	1·6010	47·6165	2·0119	−0·1810	43·595	15·8545	0·0741	−0·0066	50
1933	1·0605	49·1692	0·5611	−0·1838	62·341	16·3715	0·0207	−0·0067	51
1934	1·0095	57·7030	−3·5048	−0·2910	59·745	19·2130	−0·1291	−0·0106	47
1935	1·6195	42·8835	−5·2352	0·0639	25·410	14·2786	−0·1928	0·0023	51
1936	1·2630	35·9925	−1·3545	0·2039	52·779	11·9842	−0·0499	0·0074	46
1937	1·4620	50·6541	2·9358	−0·3345	38·297	16·8659	0·1081	−0·0122	51
1938	2·2750	26·0827	1·9640	−0·0605	39·052	8·6846	0·0723	−0·0022	50
1939	2·1495	53·0188	−3·2337	−0·0463	34·386	17·6533	−0·1191	−0·0017	50
1940	2·0250	8·0977	−0·9854	0·0419	27·826	2·6962	−0·0363	0·0015	49
1941	2·1370	28·1053	−2·4402	0·1045	51·115	9·3580	−0·0899	0·0038	49
1942	2·1645	38·0940	−2·2334	−0·2043	49·669	12·6839	−0·0823	−0·0074	49
1943	1·1695	56·9586	6·5943	−0·2475	28·152	18·9651	0·2429	0·0090	50
1945	1·6745	26·2444	−1·3426	0·0013	40·420	8·7384	−0·0494	0·0000	48
1946	2·1160	12·7970	0·4520	−0·1576	29·904	4·2609	0·0166	−0·0057	49
Mean	1·6948	38·1012	−0·4151	−0·0922	—	12·6863	−0·0153	−0·0034	—

would not be likely to be improved appreciably by the addition of further terms. Moreover, there are theoretical grounds for not carrying the regression too far. The trend of the population with time may be expected to approximate to a portion of a logistic curve: when the logarithms of the calculated values for the logistic curve, fitted to the present data and published elsewhere (Davidson & Andrewartha, 1948, Fig. 4A), were fitted to a polynomial curve of the third degree the regression accounted for all but a very small proportion of the variance (see Table 3). Accordingly, the regressions for eliminating the trend of the data with time were not carried beyond the cubic term.

Table 3. *Analysis of variance of regression of log of the calculated value for logistic curve on time*

Source of variance	Degrees of freedom	Sums of squares	Mean square
Linear term	1	2·9598	2·9598
Quadratic term	1	0·0005	0·0005
Cubic term	1	0·0029	0·0029
Total regression	3	2·9632	0·9877
Residual	16	0·0002	0·00001
Total	19	2·9634	—

At first it was intended to use the data from all the 14 years, but as it was proposed to calculate a 6-term partial regression the labour would have been heavy, and it was decided to use instead the first 8 years viz. 1932–9. The residual deviations from the trend lines provided the individual values for the dependent variate of the partial regression equation. Since the data were all expressed as logarithms, relative differences in the general level of thrips population from year to year had no influence on the results and it was appropriate to pool the data for the 8 years.

The calculations of the sums of squares and products were made by the short method using identities of the form

$$S(y-Y)^2 = Sy^2 - [nA^2 + B^2 S\xi_1^2 + C^2 S\xi_2^2 + D^2 S\xi_3^2].$$

But there were 60 intervals along the x axis for the data for the partial regression whereas the polynomials had been calculated using 20 intervals for x. The polynomial coefficients appropriate to the value $n=60$ were estimated from those calculated for $n=20$ using identities of the form

$$3\,B_{20}^2 . S_{20}\xi_1^2 = B_{60}^2 . S_{60}\xi_1^2.$$

The conversion factors which were calculated in this way were:

$$A_{60} = A_{20}, \qquad C_{60} = 0{\cdot}036831\, C_{20},$$
$$B_{60} = 0{\cdot}332963\, B_{20}, \qquad D_{60} = 0{\cdot}036460\, D_{20}.$$

In order to have an indication of the accuracy of these estimates the 60 polynomial values for one variate (x_1 for 1936) were calculated out. The sum of the 60 estimated values agreed with the sum of the observed values to 6 significant figures, and it was considered likely that little accuracy had been lost by the labour-saving device of grouping the data before calculating the polynomial. The estimated values for the polynomial coefficients for $n=60$ are given in Table 2. The number of days on which records were taken during each 60-day period are also given in the last column of the table.

The data were non-orthogonal. Since the samples of roses were not taken on Sundays, and certain other days were also missed, there were always less than 60

observations in each period of 60 days. The missing records were allowed for by adding to the original estimates of sums of squares and products a quantity calculated from expressions of the form $S(2yY - Y^2)$ for the sums of squares, and $S(Yx + yX - XY)$ for the sums of products. These expressions were summed over all the missing records.

A similar procedure was followed with the independent variates. The 60 observations for each independent variate were divided into 20 groups and regression equations were obtained by calculating orthogonal polynomials to the third degree in x (days). Residual deviations from the trend lines provided the individual values of the independent variates of the partial regression equations.

temperature and rainfall. A preliminary 3-term partial regression was calculated using data from 4 years' records and only for the day immediately before the sampling day: daily maximum air temperature, daily total rainfall and changes in the barometric pressure between 9 a.m. and 3 p.m. were chosen as the three independent variates. The partial regression of thrips on changes in barometric pressure was small and somewhat less than half its standard error. It was therefore concluded that changes in barometric pressure were not exerting any appreciable influence on the numbers of thrips in the roses over and above that which could be related to temperature and rainfall. Changes in barometric pressure were excluded from further consideration.

Table 4. *Individual sums of squares and products contributed by each year* 1932–9

Variate	1932	1933	1934	1935	1936	1937	1938	1939	Total 4 years	Total 8 years
x_1	3547·23	4438·36	3325·82	3638·66	4244·16	3484·85	2814·25	3787·28	15109·10	29280·6
x_2	1581·08	1148·65	17771·50	13339·54	7073·56	3155·82	748·54	18339·02	19225·09	63157·7
x_3	3343·57	4407·76	3033·34	2766·13	3986·55	3201·53	2616·41	3966·77	13718·99	27322·0
x_5	3117·18	3945·19	2224·22	3552·16	2797·69	3346·98	2973·52	3905·24	13961·51	25862·1
x_1x_2	−302·32	−240·66	−479·57	−45·32	−1310·45	−140·99	142·72	302·45	−729·29	−2074·1
x_1x_3	1865·48	1656·57	1223·54	1531·95	2229·59	1583·56	603·48	2537·22	6637·56	13231·3
x_1x_5	295·16	−538·78	−280·99	−861·83	360·37	−62·95	−999·45	1323·79	−1168·40	−764·6
x_2x_3	473·10	499·00	1690·43	1659·32	−568·01	272·92	9399·94	2364·71	2904·34	15791·4
x_2x_5	−58·93	294·09	627·83	646·71	352·70	820·59	250·40	1448·54	1702·46	4381·9
x_3x_5	1698·76	1522·29	1299·64	1687·30	2075·90	1639·23	525·07	2670·97	6547·58	13119·1
x_1y	12·39	48·90	−5·32	37·24	23·09	44·25	24·40	51·18	142·78	236·1
x_2y	−35·82	−37·57	−6·41	−25·68	−7·00	−4·94	−3·15	−20·23	−104·01	−140·8
x_3y	11·87	40·31	−6·09	11·88	0·34	17·04	8·17	33·07	81·10	116·5
x_5y	31·80	29·28	−15·09	−12·08	−15·08	−2·99	1·01	18·82	46·01	35·6
y	3·125	2·601	3·186	2·014	2·794	1·635	2·188	1·926	9·375	19·4

(*b*) *Selection of independent variates*

The sample of roses was taken about 9 a.m. each day. It was unlikely that appreciable movement of the thrips had taken place earlier than this: the sample may therefore be regarded as an estimate of the number of thrips in the roses at the close of the previous day. The individual roses may have been attractive to the thrips during several days before the sample was taken; in selecting independent variates for the partial regression equation it is therefore necessary to consider causes which may have been operating several days before the sample was collected.

Experience with *T. imaginis* suggested that atmospheric temperature, rainfall and possibly changes in barometric pressure may influence the activity of the insects in seeking out the flowers. Changes in barometric pressure were known to be closely associated with both atmospheric temperature and rainfall and it was possible that changes in barometric pressure may not have an appreciable influence independent of

The daily maximum atmospheric temperature, recorded 1, 2 and 3 days before the sampling day and the total daily rainfall for the same 3 days were selected as independent variates for a 6-term partial regression equation. For ease of reference these will be referred to by symbols:

- x_1 Daily maximum atmospheric temperature in degrees Fahrenheit recorded one day before the sampling day.
- x_2 Total daily rainfall in units of 0·01 in. recorded 1 day before the sampling day.
- x_3 As for x_1 but recorded 2 days before the sampling day.
- x_4 As for x_2 but recorded 2 days before the sampling day.
- x_5 As for x_1 but recorded 3 days before the sampling day.
- x_6 As for x_2 but recorded 3 days before the sampling day.

It is not practicable to publish all the data from which the regression was calculated. Fig. 2 illustrates

some of the data for 1935: the deviations of the observed values from the three trend lines represent respectively the individual values for the dependent variate (y) and the two independent variates (x_1) and (x_2) for 1935. Similarly, the individual values for the other independent variates (x_3, x_4, x_5 and x_6) were found by calculating the appropriate trend lines and taking the deviations of the observed values from them. The same process was repeated for each year under consideration. Table 4 lists the individual sums of squares and products contributed by each year and the totals from which the 'c' multipliers for the partial regression equations were calculated.

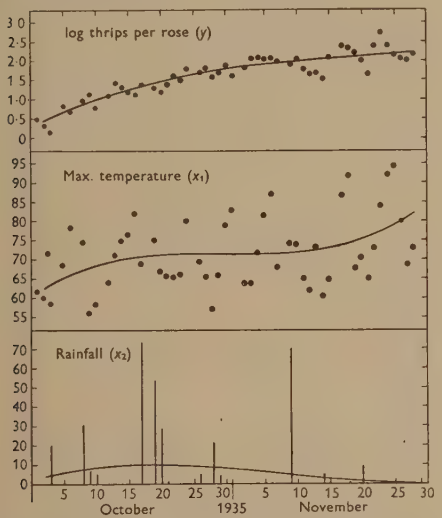

Fig. 2. The polynomial curves which were used to eliminate trend with time for y, x_1 and x_2 for 1935. They were calculated from the formulae:

$X_1 = 71{\cdot}805 + 0{\cdot}3359\ \xi_1 + 0{\cdot}008789\ \xi_2 + 0{\cdot}003627\ \xi_3$,

$X_2 = 5{\cdot}715 - 0{\cdot}2056\ \xi_1 - 0{\cdot}06132\ \xi_2 + 0{\cdot}002255\ \xi_3$,

$Y = 1{\cdot}6195 + 0{\cdot}04288\ \xi_1 - 0{\cdot}005235\ \xi_2 + 0{\cdot}00006393\ \xi_3$,

X_1 in degrees Fahrenheit; X_2 in units of 0·01 in.; Y in log thrip per rose.

Similar regressions were calculated for the other variates and for all the years 1932–9. The deviations from the curves provided the individual values for the variates in the partial regressions, calculated in § 4.

(*c*) *The partial regression of thrips numbers on maximum temperature and rainfall*

Because of the labour that would have been involved if the larger sample had been used, the 6-term partial regression was first calculated on the data for 4 years. The years 1932, 1933, 1935 and 1937 were chosen because they had the fewest missing records (see Table 2). The results are set out in Table 5. The partial regressions of y on x_4 and x_6 were small and insignificant, indicating that rain falling on the second and third day back from the sampling day was not having an appreciable influence on the numbers of thrips in the roses. These terms were excluded from the regression: the results of the new 4-term regression are set out in Table 6. The partial regressions of y on x_1 and x_2 were highly significant; the partial regression of y on x_3 was small and non-significant despite a relatively high total correlation of y on x_3 (see Table 4); the partial regression of y on x_5 though relatively small is significant at the 5 % level. These

Table 5. *Partial regressions of y on six independent variates. Calculated from data for 4 years*

	Regression coefficients		
Variate	$b \times 10^2$	S.E. $\times 10^2$	t
x_1	0·9146	0·2023	4·520
x_2	−0·5541	0·1479	3·747
x_3	0·0180	0·2420	—
x_4	−0·0817	0·1363	—
x_5	0·4830	0·2092	2·309
x_6	−0·0854	0·1220	

Analysis of variance

Source of variance	Degrees of freedom	Sums of squares	Mean square
Regression	6	2·1842	0·36403
Residual	181	7·1905	0·03973
Total	187*	9·3747	—

$Z = 1{\cdot}1077$; for $P = 0{\cdot}01$, $Z = 0{\cdot}5152$; for $P = 0{\cdot}05$, $t = 1{\cdot}960$.

* There were 203 sampling days during the 4 years: 4 degrees of freedom were lost with each polynomial calculated making 16 for the 4 years and leaving a total of 187 degrees of freedom for the partial regression.

Table 6. *Partial regressions of y on four independent variates. Calculated for data for 4 years*

	Regression coefficients		
Variate	$b \times 10^2$	S.E. $\times 10^2$	t
x_1	0·9387	0·1992	4·713
x_2	−0·5513	0·1472	3·744
x_3	0·0346	0·2300	—
x_5	0·4591	0·2066	2·222

Analysis of variance

Source of variance	Degrees of freedom	Sums of squares	Mean square
Regression	4	2·1530	0·53824
Residual	183	7·2218	0·03946
Total	187	9·3747	—

$Z = 1{\cdot}3065$; for $P = 0{\cdot}01$, $Z = 0{\cdot}5999$; for $P = 0{\cdot}05$, $t = 1{\cdot}960$.

apparent anomalies may be explained by reference to Table 4. The data indicate a positive correlation of x_3 with y and also with x_1 and x_5, and the last two are also both positively correlated with y. In other words, x_3 accounts for no appreciable part of the variance of y in addition to that which is explicable in terms of x_1 and x_5, and of these two the dependence of x_3 on x_1 is the more important. The total regression of y on x_5 is small but positive, and the partial regression is enhanced by the negative correlation between x_1 and x_5. The figures in Table 4 also indicate that the small positive regression of y on x_5 was due largely to the influence of 2 of the 4 years, namely 1932 and 1933; and the negative correlation of x_1 with x_5 was not consistent for all 4 years.

The physical explanation for these statistical results depends upon the nature of the weather in the Adelaide district. The weather is dominated by a series of cyclonic and anti-cyclonic systems which drift across the continent with considerable irregularity but with an average periodicity of somewhere between 6 and 7 days. Consequently, the temperature of any one day is likely to resemble that of the day before or the day after and to differ from that recorded 3 days before or 3 days after. The difference may still be there though less marked for readings separated by 2 days. For example, this was the case with 1933 and 1935 but not with 1932 (Table 4).

The same 4-term partial regression was recalculated from a larger sample, i.e. using the data for all the 8 years 1932–9. The four independent variates were retained, because it was considered that the more precise estimates obtained from the larger sample might be appreciably different from those calculated from the smaller sample, particularly with respect to the partial regressions of y on x_3 and x_5. The results are given in Table 7. With the larger sample the partial regression of y on x_5 has become smaller and non-significant; the partial regression of y on x_3 has become larger but is still non-significant. The data in Table 4 indicate that the change in the relative importance of x_5 may be partly due to a reduction in the size both of the negative correlation between x_1 and x_5 and the positive correlation between x_5 and y. In the light of these results, and of the discussion above, it seems likely that the results set out in Table 6 may have been unduly influenced by the inclusion of one or more 'unusual' years in the small sample.

Table 7. *Partial regression of y on four independent variates. Calculated from data for* 8 *years*

	Regression coefficients		
Variate	$b \times 10^2$	S.E. $\times 10^2$	t
x_1	0·7153	0·1626	4·400
x_2	−0·2498	0·1001	2·496
x_3	0·1693	0·2087	—
x_5	0·1154	0·1698	—

Analysis of variance

Source of variance	Degrees of freedom	Sums of squares	Mean square
Regression	4	2·2792	0·5698
Residual	360	17·1899	0·04775
Total	364*	19·4691	—

$Z = 1{\cdot}2397$; for $P = 0{\cdot}01$, $Z = 0{\cdot}5999$; for $P = 0{\cdot}01$, $t = 2{\cdot}576$.

* There were 396 sampling days altogether: since 8 polynomials were calculated 32 degrees of freedom were used up leaving a total of 364 for the partial regression.

Table 8. *Partial regression of y on three independent variates x_1, x_2 and x_3. Calculated from data for* 8 *years*

	Regression coefficients		
Variate	$b \times 10^2$	S.E. $\times 10^2$	t
x_1	0·6732	0·1502	4·481
x_2	−0·2642	0·0978	2·703
x_3	0·2534	0·1680	1·509

Analysis of variance

Source of variance	Degrees of freedom	Sums of squares	Mean square
Regression	3	2·2571	0·75236
Residual	361	17·2119	0·04768
Total	364	19·4690	—

$Z = 1{\cdot}3794$; for $P = 0{\cdot}01$, $Z = 0{\cdot}6651$; for $P = 0{\cdot}05$, $t = 1{\cdot}960$.

Table 9. *Partial regression of y on three independent variates x_1, x_2 and x_5. Calculated from data for* 8 *years*

	Regression coefficients		
Variate	$b \times 10^2$	S.E. $\times 10^2$	t
x_1	0·7967	0·1278	5·552
x_2	−0·2105	0·0875	2·405
x_5	0·1971	0·1367	1·443

Analysis of variance

Source of variance	Degrees of freedom	Sums of squares	Mean square
Regression	3	2·2478	0·7493
Residual	361	17·2212	0·04770
Total	364	19·4690	—

$Z = 1{\cdot}3770$; for $P = 0{\cdot}01$, $Z = 0{\cdot}6651$; for $P = 0{\cdot}05$, $t = 1{\cdot}960$.

Since the partial regressions of y on x_3 and x_5 account for no appreciable amount of the variance of y in addition to that which may be related to x_1 and x_2, it is best to eliminate x_3 and x_5 from the regression. But having regard to (*a*) the relatively high positive total correlation of x_3 with y, and (*b*) the significant value for the partial regression of y on x_5 given by the

earlier calculation with the smaller sample, it is instructive to eliminate x_3 and x_5 separately and to consider the two 3-term regressions which are thereby obtained. The results are set out in Tables 8 and 9. The same conclusion is indicated by the two 3-term regressions as was reached from consideration of the 4-term regression, namely, that neither x_3 nor x_5 was influential independently of x_1 and x_2.

Nevertheless, it seems likely that (due to the irregular movement of the cyclonic and anti-cyclonic systems which dominate the weather in the Adelaide district) occasionally a period may occur during which the maximum temperature registered 3 days before the sampling day may influence the number of thrips in the sample. But with the present data the best expression of the variability of the number of thrips in roses in terms of maximum temperature and rainfall is given by a 2-term partial regression in which the independent variates are daily maximum atmospheric temperature and total daily rainfall occurring on the day before the sample was taken. The figures given in Table 10 indicate (reverting now from logarithms back to the original scale) that on the average the daily number of thrips per rose increased by about 25 % for each increase of 10° F. in the daily maximum atmospheric temperature, and decreased about 66 % for each increase of 1 in. in the total daily rainfall. But daily deviations of 10 or 20° F. from the trend line were quite usual, whereas daily deviations of 1 in. or even 0·5 in. were relatively uncommon; and the β coefficients given in column 5 of Table 10 indicate that on the average changes in maximum temperature were about three times as important as changes in rainfall in influencing the numbers of thrips in the roses.

Table 10. *Partial regression of log thrips per rose on maximum temperature and rainfall. Calculated on data for* 8 *years*

	Regression coefficients			
Variate	$b \times 10^2$	S.E. $\times 10^2$	t	β*
x_1	0·7925	0·1280	6·192	0·307
x_2	−0·1969	0·0871	2·260	−0·102

Change per 1° F. = 2·5 %.
Change per 0·01 in. rain = 0·66 %.

Analysis of variance

Source of variance	Degrees of freedom	Sum of squares	Mean square	Variance (%)
Regression	2	2·1486	1·0743	10·54
Residual	362	17·3204	0·0478	—
Total	364	19·4690	—	—

$Z = 1{\cdot}5557$; for $P = 0{\cdot}01$, $Z = 0{\cdot}7636$; for $P = 0{\cdot}05$, $t = 1{\cdot}960$.

* β is used in the sense defined by Snedecor (1937); i.e.

$$\beta = b \times \frac{\sqrt{[S(x-\bar{x})^2]}}{\sqrt{[S(y-\bar{y})^2]}}.$$

The partial regression accounted for about 10 % of the variance. This was a smaller proportion than was expected. It seems likely that the residual variance was not composed entirely of errors of random sampling but also included certain other components. For example, incomplete elimination of trend with time may result in a larger residual variance: gregariousness on the part of the insects, and fluctuations in the number of roses on the hedge are other possible sources of 'error' which may have been represented in the residual variance (Davidson & Andrewartha, 1948). But probably more important than all these must be counted the absence of precise information on the behaviour of *T. imaginis*. In the absence of precise experimental data on the behaviour of the insect there is no guide to suitable quantities which might be tried as additional independent variates. For the present the 2-term regression given in Table 10 must be taken as the best expression that can be got to relate the activity of *T. imaginis* to the daily weather.

Although the partial regressions were relatively small they were significant, and it is instructive to demonstrate the influence of temperature and rainfall on the activity of the thrips since this knowledge may lead to a better understanding of the behaviour of the thrips in seeking out apple blossom during an outbreak.

The remainder of this paper will be devoted to a discussion of the annual fluctuations in the numbers of thrips i.e. the second component of the variance discussed in § 3. The daily counts of thrips per rose provide an estimate of the number of thrips in the garden. This estimate includes an 'error' due to the variable activity of the insects in seeking out the flowers. For certain purposes it may be desirable to consider the data after this 'error' has been eliminated. The partial regression set out in Table 10 provides the means for allowing for part of this 'error'. This matter will be discussed in § 6; § 5 is concerned with a discussion of the second component of the variance discussed in § 3 without regard to the 'error' introduced by the variable activity of the insects in seeking out the flowers.

5. ANNUAL FLUCTUATIONS IN THE NUMBER OF THRIPS IN THE ROSES

The number of thrips in the roses usually reached a maximum about the end of November, but the date varied from 15 November in 1939 to 13 December in 1945. The size of maximum varied from 82 in 1934 to 791 in 1939: these figures refer to the means of the 15-day period during which the thrips were most numerous. There was also appreciable variation in the

numbers present at the end of the winter and in the rate at which the population increased. It is not practicable to publish all the records in detail; Fig. 3 shows the mean curve for 14 years, in addition to the curves for 1934 and 1938 which may be taken as representing the two extremes. The curves were fitted to the logarithms of the daily counts for the 60 days preceding the 'peak' day. For 1934 the peak day was 5 December, for 1938 20 November and for the mean, 1 December. A further indication of the nature and extent of the variability of the data is given by the polynomial coefficients set out in Table 2. The mean

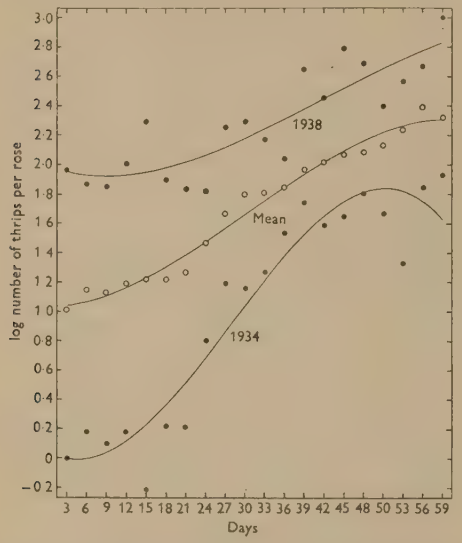

Fig. 3. The trend with time of the thrips populations for 1934, 1938, and the mean for 14 years. The observed values are the mean logarithms of the daily counts in groups of 3 days. The coefficients for the curves are given in Table 2. Thus the equation for the mean curve is

$$y = 1{\cdot}695 + 0{\cdot}0381\ \xi_1 - 0{\cdot}0042\ \xi_2 - 0{\cdot}0001\ \xi_3.$$

varied from 1·0095 to 2·2750; the linear terms were all positive but varied considerably in size; the quadratic and cubic terms were mostly negative but not consistently so: and they also varied considerably in size.

It is the purpose of this section to measure the association between the number of thrips present during the spring and early summer and certain components of the weather which had occurred during preceding months. The method of partial regression is appropriate. First it was necessary to proceed to the selection of suitable variates: as before we were guided by a knowledge of the biology of *T. imaginis* and of the weather of the Adelaide district.

(*a*) *Selection of alternative dependent variates*

It was pointed out at the beginning of § 3 that the variability in the daily records of thrips per rose may conveniently be ascribed to four components. The partial regressions which may be used to account for the variability due to annual fluctuations in the size of the thrips population will be the more satisfactory (i.e. they will account for a larger proportion of the variance) when the variance due to the other two components has been eliminated. Nevertheless, it may be necessary, for practical reasons, to ignore these components in certain instances. For example, we may require to predict the size of the thrips population at some specified time. For this purpose it was not practicable to include in the regression terms which could not be determined more than a few days in advance of the period to which the prediction applies. Hence the appropriate regressions were first calculated without 'correcting' the observed values for 'activity'.

Five quantities were selected as alternative dependent variates:

y_1 The logarithm of the geometric mean of the daily counts of thrips per rose during the fifteen days about the peak day.*

y_2 The logarithm of the geometric mean of the daily counts of thrips per rose for the 30 days preceding the peak.

y_3 As for y_2, but using the data for the 60 days preceding the peak.

y_4 The logarithm of the geometric mean of the daily counts for October.

y_5 As for y_4 but using the data for November.

These quantities provided five alternative criteria for the number of thrips present during spring and early summer. The first three were designed to allow for the variable growth of the population within each year. There is a correlation of −0·82 between the height of the peak and the date on which it occurred (Davidson & Andrewartha, 1948). So a substantial part of the variance due to growth of the population within each year was eliminated by referring y_1, y_2 and y_3 to the date of the peak rather than to a fixed calendar date. This is illustrated by the smaller variances of y_1 and y_2 compared with those of y_4 and y_5 (Table 11). The variance associated with this source was further reduced by taking a suitably short section of the growth curve. The comparison between the variances of y_1 and y_2 on the one hand, and y_3 on the other, illustrates this point. These three quantities may be regarded as alternative criteria for the number of thrips present each year about the time that the

* The 'peak day' refers to the date when the curve obtained by taking 15-day progressive means of the daily counts reached its maximum.

population reached a maximum. Whatever their respective practical merits it is clear (anticipating the results which will be presented below) that y_3 was based on too long a period for the best results statistically.

There may be practical grounds for ignoring the date when the thrips population attained greatest density and studying instead the numbers of thrips present at some specified date in the calendar year. For example, the apple trees burst into blossom at about the same time each year and it may be desirable to predict the number of thrips likely to be present at apple blossom time. The variates y_4 and y_5 represent the number of thrips present at specified times of the year irrespective of the stage of development of the population at that time.

Table 11. *Showing the variates selected for the partial regressions to measure the association between the number of thrips present during spring and the weather during preceding months*

Year	Date of 'break' of season	Independent variates					Dependent variates				
		x_1	x_2	x_3	x_4	x_5	y_1	y_2	y_3	y_4	y_5
1932	27 Mar.	8·65	12·09	4·37	6·09	13·77	2·58	2·10	1·60	1·03	2·00
1933	11 Apr.	8·94	10·42	4·39	7·04	12·09	2·02	1·57	1·06	0·78	1·76
1934	3 June	0·00	6·33	6·55	7·07	10·42	1·82	1·67	1·01	0·14	1·50
1935	14 Mar.	7·54	13·92	5·48	7·15	6·33	2·32	2·05	1·62	1·15	2·04
1936	7 Apr.	4·24	11·54	3·94	6·48	13·92	1·92	1·50	1·26	0·86	1·45
1937	28 Mar.	6·77	12·37	4·37	7·16	11·54	2·52	2·06	1·46	1·16	2·33
1938	19 Feb.	8·99	18·74	2·03	7·29	12·37	2·84	2·53	2·28	2·11	2·71
1939	24 Feb.	7·92	18·34	2·71	6·82	18·74	2·87	2·67	2·15	2·27	2·66
1940	7 Apr.	4·82	10·89	2·38	7·85	18·34	2·26	2·06	2·03	1·93	2·06
1941	3 Apr.	2·54	12·96	6·48	6·81	10·89	2·65	2·42	2·14	1·46	2·22
1942	30 Mar.	8·27	12·62	6·05	7·28	12·96	2·69	2·59	2·15	1·76	2·59
1943	7 Apr.	4·67	9·63	4·36	6·96	12·62	2·33	1·77	1·19	0·55	1·77
1944	2 Apr.	—	—	—	—	—	—	—	—	—	—
1945	4 May	2·30	8·33	6·76	6·42	9·65	2·13	1·95	1·67	1·05	1·78
1946	18 Feb.	9·92	17·69	3·28	6·43	8·33	2·34	2·30	2·11	1·91	2·21
Variance	—	9·148	13·376	2·482	0·206	11·381	0·1092	0·1445	0·2020	0·3964	0·1633

y_1 Logarithm of geometric mean of the daily records of thrips per rose for 15 days about the peak.
y_2 Logarithm of geometric mean of the daily counts of thrips per rose for the 30 days before the peak.
y_3 As for y_2, but for 60 days before the peak.
y_4 Logarithm of geometric mean of daily counts of thrips per rose during October.
y_5 As for y_4 but for November.
x_1 Total rainfall between the break of the season and 31 May (in inches).
x_2 Total effective day-degrees (in units of 100 day-degrees) from the break of the season to 31 August.
x_3 Total rainfall (in inches) for September and October.
x_4 Total effective day-degrees (in units of 100 day-degrees) for September and October.
x_5 As for x_2 but for the year preceding the one when the samples of thrips were taken.

(*b*) *Selection of independent variates*

Unlike many other insect species which occur in the same climatic region *T. imaginis* has no resting or 'resistant' stage in its life cycle. The insects are active throughout the year; during winter development is slow due to low temperature; the mortality rate is high during summer due to dryness and lack of food; but during the spring and early summer the environment is more favourable. At this time of the year adequate temperature and soil moisture favour rapid development and the survival rate is high. Food is usually more plentiful (Davidson, 1936). Pollen is essential for growth and reproduction; practically no eggs were laid by females from whose diet pollen had been excluded (Andrewartha, 1935).

The flowers of a wide variety of plants serve as hosts for *T. imaginis*, but the most important belong to a group of annual weeds which are adapted to the climate of the Adelaide area (Evans, 1932). The seeds remain dormant during the long dry summer and germinate in the autumn when the dry season gives way to the rainy winter season. The 'break' of the season is usually quite distinct: rainfall which is adequate to germinate the over-summering seeds is usually followed by sufficient rainfall to maintain the seedlings and promote their growth. The plants make vegetative growth during the autumn and produce flowers in the spring; they set seeds and die as the dry summer season develops. On those occasions when the 'break' of the season occurs early in the autumn the plants make strong vegetative growth before the low temperature of winter retards development and usually commence flowering earlier in the spring,

producing an abundance of flowers during spring and early summer. When the seasonal 'break' occurs late in the autumn the plants make little growth before the winter and the vegetative growth continues during the spring. On these occasions the plants commence flowering later and may produce a smaller crop of flowers. It may be expected that an abundance of flowers, particularly when they are present early in the spring, would favour the multiplication of *T. imaginis*.

Consequently, in selecting independent variates consideration was given to quantities which might represent the amount of growth made by the host plants of the thrips during autumn and winter. But first it was necessary to define the 'break' of the season with reference to meteorological records. The method used by Trumble (1937) to define the duration of the growing season for annual pasture species in southern Australia was adopted. Starting with the first substantial fall of rain in the autumn a progressive total of rainfall minus evaporation was calculated by adding daily rainfall and subtracting one-third of the daily evaporation from a free water surface.* Owing to the steep increase in the rate of daily rainfall and the steep decrease in the rate of daily evaporation at this time of the year there was usually a clearly defined date when the curve representing the progressive total of rainfall minus evaporation left the zero axis and remained consistently above it for the duration of the winter. This date was chosen to represent the 'break' of the season, i.e. it was considered that this was the date on which the seeds of the annual plants which are hosts for *T. imaginis* began to develop. For 10 of the 14 years the method indicated the 'break' of the season with no ambiguity. But on four occasions, namely 1937, 1938, 1941, and 1942, an unusual dry spell occurred after the apparent 'break' of the season, and the progressive total of rainfall minus evaporation remained at zero for a short period before definitely leaving the zero axis. Details of rainfall and evaporation for these periods in 1937, 1938, 1941 and 1942 are given in Table 12. From field notes kept by the farm manager at the Waite Institute, and from other considerations, it was clear that this short dry spell should be ignored and the growing season should be taken to begin with the dates indicated in the table. The estimated date of the 'break' of the season for the 14 years is given in Table 11.

It was considered unlikely that lack of rainfall during winter (June to August) would ever be critical for the growth of the host plants; but on some occasions the rainfall during autumn may have been less than optimal. Consequently, the first independent variate selected was the total rainfall recorded between the 'break' of the season and 31 May. The individual totals for the 14 years are given in inches of rainfall under the heading x_1 in Table 11.

Table 12. *Details of the rainfall and evaporation at the beginning of the growing season in* 1937, 1938, 1941 *and* 1942

Year	Date of dry spell	Duration of 'dry spell'* days	Total rain during first wet spell (in.)	Total rain during 'dry spell'* (in.)	One-third net evaporation during dry spell (in.)
1937	20–26 Apr.	7	0·99	0·04	0·25
1938	23 Mar.–15 Apr.	24	1·61	0·17	1·01
1941	14–16 Apr.	3	0·60	0·06	0·19
1942	22–26 Apr.	5	1·01	0·08	0·12

* Duration of 'dry spell' was arbitrarily defined as the period during which the progressive total rainfall minus evaporation remained at zero.

It was considered likely that the temperature experienced during the growing period would influence the amount of vegetative growth made by the host plants. The plants grow only slowly during the winter and there is probably a threshold below which no appreciable growth occurs. There was no experimental evidence to indicate where the threshold occurs with the plants under consideration and it was arbitrarily chosen at 48° F. (8·9° C.). Thus the second independent variate which was selected may be defined as the total number of 'thermal units' accumulated between the 'break' of the season and 31 August. The number of thermal units (or day-degrees) per day was calculated from the expression

$$\frac{\text{Maximum temperature} - 48}{2},$$

and the daily values were summed for all the days between the 'break' of the season and 31 August. In Table 11, under the heading x_2, the individual totals for the 14 years are given in units of 100 day-degrees.

The development of both the host plants and the thrips may be influenced by rainfall and temperature during the spring. In particular rainfall becomes less reliable as the dry season approaches and it was

* The standard Australian evaporimeter tank is used to measure evaporation at the Waite Institute. This is described in an Australian Meteorological Observers' Handbook.

considered that on occasion rainfall in the spring may have been less than optimal. Accordingly, two further quantities were selected as independent variates:

x_3 Total rainfall in inches during September and October.

x_4 Total accumulated 'thermal units' for September and October in units of 100 day-degrees.

Finally there was the possibility that the number of thrips present in the spring and early summer might have been influenced not only by the weather during the same year but also by events which had occurred the year before. For example, after a year which had favoured the strong development of host plants the seeds of these may be more numerous and more widely distributed; or there may be more thrips survive the summer and winter after a year when the insects had been more numerous. To allow for this possibility a fifth independent variate was selected:

x_5 The total 'thermal units' accumulated between the 'break' of the season and 31 August during the year preceding the sampling year.

It was not possible to select independent variates which would serve to discriminate between the influence of the weather on the host plants and its more direct influence on the insects themselves. For example, during the 'pupal' stage *T. imaginis* is susceptible to desiccation (Andrewartha, 1934): adequate soil moisture during the autumn while temperature is still adequate for development may reduce the mortality rate due to desiccation, and thus result in an increase in the size of the population at this time of the year. The records showed that there were relatively more thrips in the roses during the autumn for some years than for others (Davidson & Andrewartha, 1948). Thus the rainfall and temperature experienced in the autumn may influence the numbers of thrips present in the spring by causing an increase in the size of the autumn population with a corresponding larger initial population at the beginning of the next spring (Evans, 1934). In this case the direct influence of the weather on the insects would be operating in the same direction as the indirect influence on the host plants. During the spring when the number of niches potentially available to the thrips is increasing rapidly the multiplication of the insects may be favoured by warm dry weather which would increase the 'activity' of the thrips in seeking out new niches. But the continued development of the host plants may be favoured by moist cool weather. In this case the direct and indirect influences of the weather on the numbers of thrips may be operating in opposite directions. Considerations of this sort should be taken into account in considering the results of the partial regressions which are given below.

(*c*) *Results of partial regressions designed to account for annual fluctuations in the number of thrips in the roses*

The calculations for the partial regressions including all five independent variates were completed for only two of the dependent variates, namely y_1 and y_2. The results are set out in Tables 13 and 14. The regression with y_1 was barely significant; that for y_2 was significant at the 1 % level. In both cases the more important terms were x_2, x_3 and x_5. The coefficient b_1 was small and less than half its standard error. Apparently the amount of rain falling during autumn contributed no appreciable influence additional to that which could be attributed to the other four variates. So x_1 was eliminated giving a series of new partial regressions with four independent variates; these were calculated out for all five of the dependent variates. The results are given in Tables 15, 17–19 and 21.

Table 13. *Partial regressions of y_1 on x_1, x_2, x_3, x_4 and x_5*

	Regression coefficients		
Variate	*b*	S.E.	*t*
x_1	0·0199	0·0295	—
x_2	0·0903	0·0258	3·507
x_3	0·1514	0·0658	2·303
x_4	0·1041	0·1369	—
x_5	0·0503	0·0230	2·186

Analysis of variance

Source of variance	Degrees of freedom	Sum of squares	Mean square	Variance (%)
Regression	5	1·06000	0·2120	58·8
Residual	8	0·35600	0·0450	—
Total	13	1·420	—	—

$Z=0·7750$; for $P=0·05$, $Z=0·6525$; for $P=0·05$, $t=2·306$.

Table 14. *Partial regressions of y_2 on x_1, x_2, x_3, x_4 and x_5*

	Regression coefficients		
Variate	*b*	S.E.	*t*
x_1	0·0027	0·0274	—
x_2	0·1267	0·0239	5·297
x_3	0·2091	0·0611	3·423
x_4	0·1918	0·1271	1·509
x_5	0·0527	0·0214	2·463

Analysis of variance

Source of variance	Degrees of freedom	Sum of squares	Mean square	Variance (%)
Regression	5	1·56837	0·3137	73·1
Residual	8	0·31063	0·0388	—
Total	13	1·879	—	—

$Z=1·0446$; for $P=0·01$, $Z=0·9459$; for $P=0·01$, $t=3·355$.

When y_1 (the mean log of the number of thrips present during the 15 days about the maximum of the population curve) was taken as a criterion of the density of the population the partial regression containing the four terms x_2, x_3, x_4 and x_5 was significant at the 5 % level (Table 15). But it was clear that x_4 contributed nothing to the value of the regression. So x_4 was eliminated leaving x_2, x_3 and x_5.

Table 15. *Showing the partial regression of y_1 on x_2, x_3, x_4 and x_5*

	Regression coefficients		
Variate	b	S.E.	t
x_2	0·0988	0·0218	4·533
x_3	0·1376	0·0606	2·272
x_4	0·0971	0·1323	—
x_5	0·0470	0·0218	2·155

Analysis of variance

Source of variance	Degrees of freedom	Sum of squares	Mean square	Variance (%)
Regression	4	1·03953	0·2599	61·3
Residual	9	0·38047	0·0423	—
Total	13	1·420	—	—

$Z=0·9077$; for $P=0·01$, $Z=0·9299$, $t=3·250$; for $P=0·05$, $t=2·262$.

The three-term partial regression was now significant at the 1 % level and each term was individually significant at the 5 % level or better (Table 16). This three-term regression (which accounted for 63 % of the variance of y_1) was the best expression of the relationship between the numbers of thrips and their physical environment which could be got when y_1 was used as a criterion of density of the thrips population.

When y_2 (the mean log of the number of thrips present during the 30 days preceding the maximum of the population curve) was used the partial regression containing the four terms x_2, x_3, x_4 and x_5 was significant at the 1 % level; three of the four terms were individually significant at the 5 % level or better, and b_4 exceeded its standard error in the ratio 1·6; the regression accounted for 76 % of the total variance of y_2 (Table 17). When x_4 was excluded the resulting three-term regression was rather more significant ($Z=1·257$), but accounted for rather less of the total variance (72 %). Thus little, if anything, was to be gained by dispensing with x_4 and it was considered that the four-term regression given in Table 17 was the best expression of the relationship between the numbers of thrips and their physical environment that could be got when y_2 was used as a criterion of the density of the thrips population.

The partial regression of y_3 (mean log of the number of thrips present during the 60 days preceding the maximum of the population curve) on x_2, x_3, x_4 and x_5 is given in Table 18. The regression was significant at the 5 % level: but x_2 was the only term which was individually significant: and the regression accounted for only 56 % of the total variance of y_3. When x_4 was excluded the relationship was slightly improved ($Z=0·9268$ $P<0·05>0·01$), but x_2 was still the only term which was individually significant. Since y_3 was thus shown to be less satisfactory, on statistical grounds, than either y_1 or y_2, and as there was no biological reason for preferring y_3 to y_1 or y_2, y_3 was not considered any further.

Table 16. *Showing the partial regression of y_1 on x_2, x_3 and x_5*

	Regression coefficients			
Variate	b	S.E.	t	β*
x_2	0·0960	0·0210	4·579	1·063
x_3	0·1290	0·0580	2·223	0·615
x_5	0·0483	0·0212	2·277	0·493

Increase per unit increase in x_2 = 31·9 %†
Increase per unit increase in x_3 = 42·8 %
Increase per unit increase in x_5 = 16·0 %

Analysis of variance

Source of variance	Degrees of freedom	Sum of squares	Mean square	Variance (%)
Regression	3	1·01673	0·3389	63·1
Residual	10	0·40327	0·0403	—
Total	13	1·420	—	—

$Z=1·0645$; for $P=0·01$, $Z=0·9399$, $t=3·169$; for $P=0·05$, $t=2·228$.

* $\beta = b \times \frac{\text{S.D. of } x}{\text{S.D. of } y}$.

† Percentage increase $= \frac{100\,b}{0·3010}$.

Table 17. *Showing the partial regression of y_2 on x_2, x_3, x_4 and x_5*

	Regression coefficients		
Variate	b	S.E.	t
x_2	0·1278	0·0197	6·490
x_3	0·2072	0·0548	3·784
x_4	0·1909	0·1196	1·596
x_5	0·0522	0·0197	2·652

Analysis of variance

Source of variance	Degrees of freedom	Sum of squares	Mean square	Variance (%)
Regression	4	1·56802	0·3920	76·1
Residual	9	0·31097	0·0346	—
Total	13	1·879	—	—

$Z=1·2146$; for $P=0·01$, $Z=0·9299$, $t=3·250$; for $P=0·05$, $t=2·262$.

The remaining two independent variates which were chosen as criteria of the number of thrips present ignored the date of the maximum of the population curve and thus included a substantial part of the variance due to natural increase of the population within each year. The regression of y_4 (mean log of the number of thrips during October) on x_2, x_3, x_4 and x_5 is given in Table 19. The regression was significant at the 1% level and accounted for 75% of the variance of y_4: but x_2 was the only term which was individually significant. With the progressive elimination of x_3, x_4 and x_5 the significance of the regression was increased. The total regression of y_4 on x_2 was significant at the 0·1% level and the regression accounted for 66% of the variance of y_4 (Table 20).

The partial regression of y_5 (mean log of the number of thrips during November) on x_2, x_3, x_4 and x_5 is given in Table 21. The regression was significant at the 1% level: and the regression accounted for 77% of the total variance. Three of the four terms were individually significant at the 5% level or better, and the fourth (b_5) exceeded its standard error in the ratio of nearly 2. When x_5 was excluded the resulting three-term regression was less significant ($Z=1·197$): and the regression accounted for less of the total variance of y_5 (70%). The four-term regression given in Table 21 was therefore the best expression of the relationship between the physical environment and the number of thrips present during November.

Table 18. *Partial regression of y_3 on x_2, x_3, x_4 and x_5*

	Regression coefficients		
Variate	*b*	S.E.	*t*
x_2	0·1313	0·0315	4·170
x_3	0·1690	0·0875	1·932
x_4	0·2152	0·1911	—
x_5	0·0477	0·0315	1·516

Analysis of variance

Source of variance	Degrees of freedom	Sum of squares	Mean square	Variance (%)
Regression	4	1·83189	0·4580	56·3
Residual	9	0·79411	0·0882	—
Total	13	2·626	—	—

$Z=0·8233$; for $P=0·01$, $Z=0·9299$, $t=3·250$; for $P=0·05$, $Z=0·6450$, $t=2·262$.

Table 19. *Partial regression of y_4 on x_2, x_3, x_4 and x_5*

	Regression coefficients		
Variate	*b*	S.E.	*t*
x_2	0·1668	0·0335	4·983
x_3	0·1140	0·0930	1·226
x_4	0·3100	0·2033	1·525
x_5	0·0680	0·0335	2·032

Analysis of variance

Source of variance	Degrees of freedom	Sum of squares	Mean squares	Variance (%)
Regression	4	4·25473	1·0637	74·8
Residual	9	0·89827	0·0998	—
Total	13	5·153	—	—

$Z=1·1833$; for $P=0·01$, $Z=0·9299$, $t=3·250$; for $P=0·05$, $t=2·262$.

Table 20. *Showing total regression of y_4 on x_2*

	Regression coefficient		
Variate	*b*	S.E.	*t*
x_2	0·1425	0·0279	5·105

Percentage increase per unit increase of $x_2=47·3$%

Analysis of variance

Source of variance	Degrees of freedom	Sum of squares	Mean square	Variance (%)
Regression	1	3·52839	3·5284	65·8
Residual	12	1·62461	0·1354	—
Total	13	5·153	—	—

$Z=1·6302$; for $P=0·01$, $Z=1·1166$, $t=3·055$.

Table 21. *Partial regression of y_5 on x_2, x_3, x_4 and x_5*

	Regression coefficients		
Variate	*b*	S.E.	*t*
x_2	0·1247	0·0208	6·002
x_3	0·1530	0·0577	2·651
x_4	0·3156	0·1261	2·502
x_5	0·0405	0·0208	1·953

Analysis of variance

Source of variance	Degrees of freedom	Sum of squares	Mean square	Variance (%)
Regression	4	1·77712	0·4443	76·5
Residual	9	0·34588	0·0384	—
Total	13	2·123	—	—

$Z=1·2238$; for $P=0·01$, $Z=0·9299$, $t=3·250$; for $P=0·05$, $t=2·262$.

All the dependent variates (y_1 to y_5) used in this section included in themselves the variability associated with the variable 'activity' of the thrips in seeking out the roses. In the next section we shall show how some of the variability due to this cause may be eliminated and shall calculate two new quantities which may be regarded as improved estimates of the true density of the thrips population in the garden.

6. ANNUAL FLUCTUATIONS IN THE NUMBERS OF THRIPS AFTER THE ELIMINATION OF VARIANCE DUE TO 'ACTIVITY'

The methods employed in § 5 may provide the best information that can be got for the purpose of predicting the numbers of thrips likely to be present during the spring and early summer. But more precise information about the physical ecology of *T. imaginis* may be obtained by first eliminating the variance associated with the activity of the insects in seeking out the flowers. In other words, the estimate of the number of thrips present which was got by counting the number of thrips in the roses may be improved by subtracting a correction factor calculated from the regression equation obtained in § 4.

(*a*) *Calculation of the correction factor*

Each daily record of the number of thrips per rose may be considered to consist of two components: one component related to the 'real' number of thrips in the garden, the other to the activity of the thrips in seeking out the flowers. This may be written in symbols:

$$Y_{\text{observed}} = Y_{\text{real}} + Y_{\text{activity}}$$

or

$$Y_{\text{real}} = Y_{\text{observed}} - Y_{\text{activity}}.$$

The component $Y_{\text{act.}}$ was calculated by substitution in the regression equation obtained in § 4 (see Table 10):

$$Y_{\text{act.}} = 0{\cdot}007925\, x_1 - 0{\cdot}001969\, x_2. \qquad \text{(i)}$$

In this equation all the quantities $Y_{\text{act.}}$, x_1 and x_2 are written about their means, and they are all deviations from the appropriate polynomial curves, calculated from the equations:

$$1000\, Y = 1694{\cdot}75 + 12{\cdot}6863\, \xi_1 - 0{\cdot}015287\, \xi_2 - 0{\cdot}0033618\, \xi_3, \qquad \text{(ii)}$$

$$1000\, X_1 = 71401{\cdot}80 + 88{\cdot}6804\, \xi_1 + 8{\cdot}37664\, \xi_2 + 0{\cdot}012072\, \xi_3, \qquad \text{(iii)}$$

$$1000\, X_2 = 5488{\cdot}60 - 25{\cdot}1385\, \xi_1 - 0{\cdot}88726\, \xi_2 + 0{\cdot}020080\, \xi_3. \qquad \text{(iv)}$$

The coefficients for the equation for Y are means of the 14 values given in Table 2 under the heading '$n = 60$': those for X_1 and X_2 were derived in the same way from the data for x_1 and x_2. Since the means of the deviations from the curves represented by equations (ii), (iii) and (iv) were zero the quantities in equation (i) were simply the actual deviations from the appropriate mean polynomial curves: and the equation may be written

$$Y_{\text{act.}} = 0{\cdot}007925\, (x_1 - X_1) - 0{\cdot}001969\, (x_2 - X_2).$$

(*b*) *Selection of dependent variates*

The quantity $Y_{\text{act.}}$ was calculated for each day: there were 14 sets of 60 values to be calculated, one set of 60 for each year. The daily values of $Y_{\text{act.}}$ were then subtracted from the daily values of $Y_{\text{obs.}}$ to give a set of daily values for Y_{real}. The estimated values of Y_{real} were then substituted for the logarithms of the original daily counts and two new dependent variates were calculated, one related to the peak of the thrips population curve, the other to a fixed calendar date. These were:

y'_2 The logarithm of the geometric mean number of thrips per rose for the 30 days preceding the peak: using values for Y_{real} instead of $Y_{\text{obs.}}$.

y'_6 The logarithm of the geometric mean number of thrips per rose during the 30 days 17 October to 15 November: using values for Y_{real} in place of $Y_{\text{obs.}}$.

The individual values of y'_2 and y'_6 for the 14 years are shown in Table 22: the values for y_2 are included so that they may be compared with those for y'_2. The variate y'_2 is the counterpart of the variate y_2 which was used in § 5 except that the former has been 'corrected' for the influence of maximum temperature and rainfall on the activity of the thrips in seeking out the flowers. The regressions calculated with y'_2 will therefore be not only a more precise estimate of the relationship between the number of thrips and their environment, but by comparison with the regressions obtained with y_2 will also indicate the extent of the precision gained by the elimination of part of the variance associated with the activity of insects in seeking out the flowers. The variate y'_6 has no counterpart in § 5 for the very practical reason that it had to be chosen from a period which was wholly included in every one of the fourteen 60-day periods used for calculating the regression in Table 10. Since the earliest of these periods lasted from 17 September to 15 November (1939) and the latest from 15 October to 13 December (1946) it was not possible to include either the whole of October or the whole of November. The 30-day period 17 October to 15 November was chosen as a compromise.

Table 22. *Individual values for y_2, y'_2 and y'_6*

Variate	1932	1933	1934	1935	1936	1937	1938	1939	1940	1941	1942	1943	1945	1946
y_2	2·10	1·57	1·67	2·05	1·50	2·06	2·53	2·67	2·06	2·42	2·59	1·77	1·95	2·30
y'_2	2·08	1·57	1·65	2·03	1·54	2·04	2·51	2·72	2·10	2·40	2·57	1·79	1·93	2·28
y'_6	1·44	1·32	0·79	1·70	1·18	1·80	2·41	2·73	2·05	1·84	2·22	1·03	1·47	2·01

(c) Results of regressions calculated with corrected estimates of the density of the thrips population

The partial regression of y'_2 (corrected estimate of the number of thrips during the 30 days before the maximum of the population curve) on x_2, x_3, x_4 and x_5 is given in Table 23. The regression was significant at the 0·1 % level: two of the terms were individually

Table 23. *Partial regression of y'_2 on x_2, x_3, x_4 and x_5*

Variate	Regression coefficients			
	b	S.E.	t	β
x_2	0·1254	0·0185	6·79	1·224
x_3	0·2019	0·0514	3·93	0·848
x_4	0·1866	0·1122	1·66	0·226
x_5	0·0580	0·0185	3·08	0·511

Increase per unit increase in x_2 = 41·7 %
Increase per unit increase in x_3 = 67·1 %
Increase per unit increase in x_4 = 62·0 %
Increase per unit increase in x_5 = 18·9 %

Analysis of variance

Source of variance	Degrees of freedom	Sum of squares	Mean square	Variance (%)
Regression	4	1·5537	0·3884	78·4
Residual	9	0·2736	0·0304	—
Total	13	1·8273	—	—

$Z = 1·2739$, $P < 0·001$.

Table 24. *Partial regression of y'_6 on x_2, x_3, x_4 and x_5*

Variate	Regression coefficients			
	b	S.E.	t	β
x_2	0·1632	0·0229	7·13	1·091
x_3	0·1709	0·0636	2·69	0·492
x_4	0·3616	0·1389	2·60	0·300
x_5	0·0698	0·0229	3·05	0·430

Increase per unit increase in x_2 = 54·2 %
Increase per unit increase in x_3 = 56·8 %
Increase per unit increase in x_4 = 120·0 %
Increase per unit increase in x_5 = 23·2 %

Analysis of variance

Source of variance	Degrees of freedom	Sum of squares	Mean square	Variance (%)
Regression	4	3·4694	0·8674	84·4
Residual	9	0·4198	0·0466	—
Total	13	3·8892	—	—

$Z = 1·4621$, $P < 0·001$.

significant at the 1 % level, b_5 was significant at the 2 % level, and b_4 though not individually significant exceeded its standard error in the ratio 1·66. The regression accounted for 78 % of the variance of y'_2. The three-term regression from which x_4 had been excluded was slightly more significant ($Z = 1·3079$): and all the terms were individually significant at the 2 % level or better: but the regression accounted for rather less of the total variance (74 %). There was therefore little, if anything, to be gained by discarding x_4 and it was considered that the four-term regression given in Table 23 was the best expression of the relationship between the number of thrips and their environment that could be got when y'_2 was used as a criterion of the density of the thrips population.

The regression of y'_6 on x_2, x_3, x_4 and x_5 is given in Table 24. The regression was significant at the 0·1 % level: all the terms were individually significant at the 5 % level or better: and the regression accounted for 84 % of the total variance of y'_6. This was the most precise of all the relationships which have been derived in this paper judged not only by the significance of the regression as a whole ($Z = 1·4621$), and the significance of all the individual terms, but also by the proportion of the variance which the regression accounted for.

7. DISCUSSION

The influence of daily maximum temperature and daily rainfall on the activity of the thrips seeking out the flowers was discussed in § 4. The results presented in §§ 5 and 6 will be discussed under four headings.

(a) Alternative criteria for the density of the thrips population

Seven different quantities were used as alternative criteria for the density of the thrips population. Each is to be judged by a dual standard: it is relevant to ask of each how much information it gives of biological or practical matters, and how well it serves the purpose of statistical analysis. For example, if it is required to predict the number of thrips likely to be present on some future occasion, quantities like y'_2 or y'_6 will be of little interest since the correction factor for these cannot be calculated in advance. Similarly, quantities like y_1 or y_2 are of limited interest since the date of the maximum of the population curve cannot be known in advance. With *T. imaginis* the chief interest in prediction may centre around the time when the apple blossom is present; this is usually October. For other purposes it may be desirable to know the number of thrips likely to be present during November. Thus, for the practical purpose of prediction, the quantities y_4 and y_5 may prove most instructive.

But in seeking information about the ecology of *T. imaginis* it may be better to consider the density of the population about the time when it is at a maximum each year rather than during any arbitrary calendar period. The quantities which may serve this purpose are y_1, y_2 and y'_2. In this paper our chief purpose has

been to explain the fluctuations in the growth of the population from year to year. The quantity y_1 may therefore not be the best criterion to choose since it is made up from an equal number of records taken before and after the maximum of the curve. The records taken after the maximum may reflect the influence of components in the environment directly associated with the decline of the population; and these may be quite different from those associated with its growth. The quantity y_2 may therefore be preferred to y_1 since it is made up entirely from records which were taken while the population curve was ascending, being in fact the mean of the 30 days preceding the maximum of the curve. The choice between y_2 and y'_2 needs to be made on statistical grounds since biologically the two quantities are exactly equivalent.

Of the several quantities related to the maximum of the population curve, y_3 was the least satisfactory on statistical grounds. The variance was greater than that of y_1 or y_2, doubtless because y_3 was calculated from the 60 days before the maximum of the curve and therefore included more of the variance due to variable growth within each year. The greater variance of y_3 was not offset by any stronger association with the independent variates and therefore the regression with y_3 was less precise than those with y_1 or y_2 (Tables 11, 17 and 18). The quantity y_1 was less satisfactory than y_2. The variance of y_1 was less than that of y_2 (Table 11), but this was more than offset by the weaker association of y_1 with the independent variates. (Compare the total sums of squares and residual sums of squares in Tables 15 and 17.) This was doubtless due to the inclusion in y_1 of records taken when the population was beginning to decline, whereas the independent variates were all chosen to explain the growth of the population. The regression calculated with y_2 was inferior to that with y'_2 doubtless because the latter was a better estimate of the number of thrips in the garden. The residual variance of y_2 was swollen by the retention of more of the variance due to 'activity' of the insects (compare residual mean squares in Tables 17 and 23). Thus of all the quantities related to the maximum of the population, y'_2 was the best on statistical grounds.

The regression given for y'_6 was statistically the most significant of all. This was largely due to the increased strength of the relationship between x_4 and y'_6 (compare the β coefficients, for example, in Tables 23 and 24). The partial regression of y'_6 on x_4 was larger than that of y'_2 on x_4, because both y'_6 and x_4 are related to calendar dates whereas y'_2 is related to the date of the maximum of the population curve which varied from 15 November in 1939 to 13 December in 1946. The least satisfactory (on statistical grounds) of all the alternative dependent variates was y_4. The number of thrips present during October was more variable than at any other time (see Table 11). It was not possible to demonstrate a significant association between y_4 and any of the individual components of the physical environment except x_2: and the regression of y_4 on x_2 accounted for no more than 66% of the total variance of x_4 (Table 20). Nevertheless, y_4 has been retained because it is the most instructive quantity that could be selected for the practical purpose of prediction.

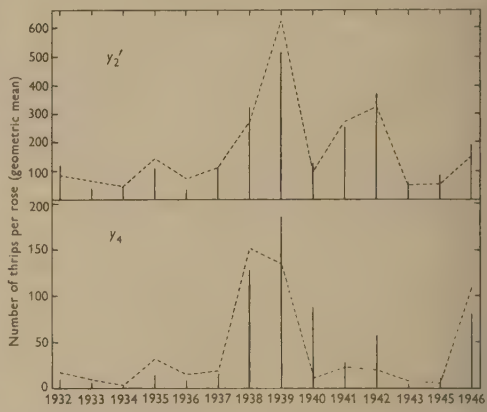

Fig. 4. The columns represent the geometric means of the daily counts of thrips per rose. The curves represent the estimated values for the same quantities calculated from the appropriate regression equations:

$$\log Y'_2 = -2{\cdot}390 + 0{\cdot}125\,x_2 + 0{\cdot}202\,x_3 + 0{\cdot}187\,x_4 + 0{\cdot}058\,x_5,$$

$$\log Y_4 = -0{\cdot}492 + 0{\cdot}142\,x_2.$$

In Fig. 4 the estimated and observed values for y'_2 and y_4 have been plotted. The agreement between the estimated and observed values for y'_2 is remarkable; for y_4 the agreement is not so close. The estimated values for y'_2 were got by substitution in the equation

$$\log Y'_2 = -2{\cdot}390 + 0{\cdot}125\,x_2 + 0{\cdot}202\,x_3 + 0{\cdot}187\,x_4 + 0{\cdot}058\,x_5,$$

which may be constructed from the information in Tables 11, 22 and 23. The estimated value for y_4 was got by substitution in the equation

$$\log Y_4 = -0{\cdot}492 + 0{\cdot}142\,x_2,$$

which may be constructed from the information in Tables 11 and 20.

The discussion which follows in §§ (*b*), (*c*) and (*d*) below has been based chiefly on the results of the regressions with y'_2, since this quantity is the most instructive on biological grounds and is to be preferred on statistical grounds to y_1, y_2 and y_3.

(b) Relative importance of different components of the physical environment

The density of the thrips population was influenced more by x_2 than by any other component of the physical environment. The β coefficients in Table 23 show that x_2 was about 1·5 times as influential as x_3, 5·4 times as influential as x_4, and 2·4 times as influential as x_5. The quantity x_2 was calculated by summing accumulated 'effective' temperature from the date of the 'break' of the season at the end of the autumn up to 31 August (see p. 210). Since temperature was considerably higher during autumn than during winter the size of x_2 was largely determined by the date of the 'break' of the season (see Table 11). When this occurred early x_2 was large. The biological significance of an early 'break' to the season was that it allowed the seeds of the annual plants which serve as hosts for *T. imaginis* to germinate early. The plants were then able to make strong growth before and during the winter and were ready to burst into flower as soon as the temperature began to rise in the spring. On the other hand, when germination was delayed by a late 'break' to the season the plants were still relatively immature at the end of winter and continued their vegetative growth as temperature increased during the spring. On these occasions flowering was delayed until late in the spring.

Since *T. imaginis* requires pollen for growth and reproduction, and since the mortality rate of the pupal stages may be high when soil moisture is inadequate, the favourable period for the multiplication of the insect was limited at the one end by the date in the spring when pollen became available in quantity and at the other end by the onset (about the end of November) of the dry summer season. It becomes clear that the close association of x_2 with the maximum density attained by the thrips population may be largely due to the value of x_2 as an indication of the date when pollen first became available in quantity in the spring, and thus as a measure of the duration of the favourable period for multiplication. This conception is illustrated in Fig. 5.

The broken lines in the figure were obtained by taking 15-day moving averages of the daily records of the number of thrips per rose, starting from the day when the population began to decline. The smooth curve is a hypothetical logistic curve.

It was shown that the lower portion of a logistic curve provided an adequate empirical fit to the data representing the mean growth of the population during the period September to December (Davidson & Andrewartha, 1948). The calculation was not carried beyond the point of inflexion of the curve because empirical data were not available beyond this point. Usually the onset of the summer drought calls a halt to the multiplication of the insects long before the population has had time to saturate its environment; empirical data on which to base a more complete curve are thus unobtainable.

The extrapolated curve which is given in Fig. 5 is therefore hypothetical. It is given because it is convenient to imagine the maximum density attained by the population each year as an ordinate on some (hypothetical) logistic curve. The height of the ordinate can then be seen to be determined by the value on the abscissa of the logistic curve which corresponds to the date when the population began to decline. In those years when this date corresponded to a high value on the abscissa the curve may be imagined as having had its origin earlier in the spring, and vice versa.

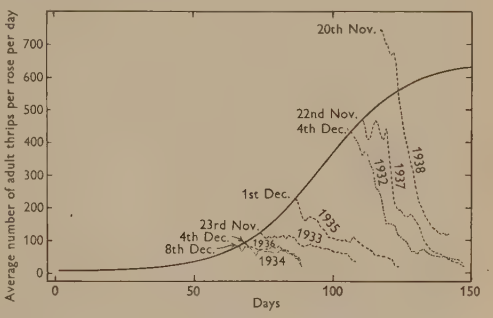

Fig. 5. Presenting a hypothetical explanation for the control of the population density by 'density-independent' components of the environment. The trend line is a hypothetical logistic curve. The broken lines are the descending parts of the observed population curves for each of the 7 years 1932–8. Each one has been moved along the abscissa so that its maximum will coincide with the hypothetical trend line. For further explanation see text.

This hypothesis is not capable of being demonstrated empirically, but it is consistent with two major facts established in § 6: (*a*) four 'density-independent' components of the physical environment accounted for 78 % of the variance of the maximum annual density of the population; (*b*) the most important individual component was x_2 which has been shown to serve as a measure of the earliness of appearance of blossoms on the plants which serve as hosts for *T. imaginis*.

The relatively large value for the maximum density attained in 1938, which exceeds the upper asymptote of the theoretical curve, may not be taken to indicate that in this year the insects may have saturated the environment. To argue that would be to attribute an empirical value to the diagram which it does not possess. Indeed it is likely that the potentialities of the environment may vary from year to

year.* In 1938 the 'potential' maximum population may have been much higher than the observed maximum (Davidson & Andrewartha, 1948).

The influence of x_2 may not have been restricted to its relationship with the duration of the favourable period for multiplication. Two other possible influences are: (*a*) when the plants made vigorous growth early they may have produced more flowers in addition to producing them earlier; (*b*) usually the chief hazard for the insects during the summer is inadequate soil moisture. Rain falling early in the autumn may alleviate this hazard and allow a small increase in the population at this time of the year, with the result that there may be a larger initial population at the beginning of the next spring (Evans, 1934). The data did not permit of these several components being measured separately and the partial regression given for x_2 represents the influence of the sum of them all. But it is considered that the most influential component was the one associated with the growth of the host plants, and the tendency for the date on which they came into blossom to be advanced on those occasions when x_2 was large and retarded when x_2 was small.

Since the value for x_2 was largely determined by the date of the 'break' of the season we may conclude that the maximum density of the population in the spring was largely determined by the weather during the previous autumn; but the significance of the partial regressions for x_3 and x_4 show that the weather during the spring may modify the tendencies established during the autumn. This is illustrated in Fig. 4. Consider, for example, the data for 1942 and 1946. In 1942 the value for x_2 was small but the population attained a moderate density because x_3 and x_4 were both large; in 1946 the value for x_2 was large but this was offset by low values for x_3 and x_4 (see Table 11). With Y_4 the calculated values were obtained from x_2 alone, and the regression largely underestimated the numbers of thrips in 1942 and overestimated them in 1946 (Fig. 4, lower curve).

The β coefficients in Table 23 show that x_3 was the second most influential component. The value for x_3 was calculated by summing the total rainfall for September and October. At this time of the year temperature and evaporation normally increase and rainfall is required to maintain adequate soil moisture. With favourable soil moisture the mortality rate of the pupal stages of *T. imaginis* may be reduced and the development of the host plants may be promoted. The data did not permit the influence of these two components to be estimated separately. Both will contribute to a positive regression of y on x_3 and it is considered that the direct influence of soil moisture on the survival rate of the insects in the pupal stage may have been more important than its indirect influence through the host plants.

During the period September–October the number of niches available to *T. imaginis* increases enormously. The multiplication of the insect may be favoured by increased activity in seeking out new situations. It was shown in § 4 that rainfall reduces activity. Thus the regression of y on x_3 will contain a negative component associated with the activity of the insects in seeking out new situations. This means that the values given for b_3 underestimate the influence of soil moisture during September–October on the maximum density of the population.

The least important component (excluding x_1) was x_4, which measured the influence of temperature during September–October. Increasing temperature will reflect an increase in the rate of development of the insect (Andrewartha, 1936), an increase in its activity in seeking out new situations, and an increase in the rate of development of the host plants. The sum of the influence of all these phenomena will be represented by the regression of y on x_4; each of them will contribute a positive component to the regression, and experience does not suggest any influence which might contribute a negative component. Nevertheless, x_4 was the least influential of all the independent variates. Apparently temperature during September–October was usually adequate, and the fluctuations which occurred were not reflected in large changes in the density of the thrips population.

The significant regression of y on x_5 was interesting because it demonstrated a residual influence carried over from the year before. Again the data did not permit of the partitioning of x_5 into further components. Since x_5 was derived from the same quantities as x_2 but for one year earlier, and since x_2 was shown to be closely related to the density of the thrips population, the influence of x_5 might be attributed to its association with the thrips population of the year before. That is there might have been a large initial population of thrips at the beginning of the spring on those occasions when x_5 was large. This association was not apparent from the data. Considering the enormous mortality which occurred each summer it seems unlikely that the chief component of x_5 was its influence on the residual number of thrips. It is more likely that x_5 may have exercised its chief influence through the host plants. Since a large value for x_2 favoured the strong development of the host plants, it is likely that seeds would be more numerous and more widespread on those occasions when x_5 was large.

But the data neither confirm nor deny these speculations. They merely indicate that the sum of the influences represented by x_5 was the third most important of the four components of the physical environment which between them accounted for

* In this connexion consider also the discussion given below on the influence of x_5.

78% of the total variance of the annual maximum density attained by the thrips population.

(c) *Secular rhythm in the annual maximum density of the population*

The observed values for y'_2 plotted in Fig. 4 indicate that the maximum density of the population tended to increase progressively for 3 or 4 years and then to decrease abruptly in the course of 1 year to a very low level from which it then gradually increased again. There was an outbreak of *T. imaginis* in 1931. So the population was known to be larger in 1931 than in either 1930 or 1932. Thus maxima occurred in 1931, 1935, 1939, 1942 and 1946. The only exception to the rule that the decline occupied only 1 year occurred after the outbreak of 1931. The average distance between maxima is 3·75 years. Do these data indicate that rhythm of the sort indicated in the sample is characteristic of the population of *T. imaginis* living in the Adelaide district?

The hypothesis which fits the observations most closely is that the density of the population was increasing progressively for 3 years and then declining abruptly every fourth year. If in such a hypothetical population we subtract the record for each year from the one ahead of it, positive and negative differences between the pairs of years would occur in the ratio of 3 positive to 1 negative. If, on the other hand, the quantities were occurring at random with respect to time there would be an equal number of positive and negative differences, and the distribution of groups of 4 differences would have the form: in every 120 trials there would be 1 group with 0 positive and 4 negative, 26 groups with 1 positive and 3 negative, 66 with 2 positive and 2 negative, 26 with 3 positive and 1 negative, and 1 group with 4 positive and 0 negative. This distribution has a mean of 2 positive (or negative) differences and a variance of 0·5. The standard error of a mean of 3·5 groups is thus $\sqrt{(0{\cdot}5/3{\cdot}5)} = 0{\cdot}378$.

In the sample under consideration there were 9 positive and 5 negative differences (1944 being missing), giving a mean of 2·571 positive for a sample of 3·5 groups of 4. This differs from 2 by 0·571 which exceeds 0·378 in the ratio 1·51. A difference of this magnitude would have occurred in 13% of random samples in which an excess of positive or negative differences was equally likely. But we have excluded (by hypothesis) the possibility of runs of negative differences and must therefore divide this probability by 2. A series of similar random samples of 15 years taken from a population in which the fluctuations were quite random with respect to time might have shown as much or more 'rhythm' as the present sample on 6 or 7 occasions in every 100. Thus the 'rhythm' shown in this sample is suggestive but does not provide conclusive evidence that oscillations of this sort are characteristic of the population of *T. imaginis* living in the Adelaide district.

Nevertheless, in this particular sample of 15 years, there was a rhythmic oscillation in the maximum density attained by the population. Periodic oscillations in a population have sometimes been related to the presence of predators in the environment (Nicholson, 1933; Smith, 1939). In the present instance no predators, parasites nor diseases of any importance were observed. Moreover, 78% of the variance was related to four quantities which were derived entirely from meteorological records: and there is no evidence that any of the four terms in the regression concealed in themselves the influence of any competitor or predator of *T. imaginis*. A substantial part of the remaining 22% is doubtless to be attributed to variance of sampling and departures from linear regression, leaving little that could be attributed to any other component of the environment whether physical or biotic.

Apart from periodic oscillations in the density of the population there is also the possibility that the maximum density of the population may have been changing slowly with time. To test this possibility orthogonal polynomials were calculated up to the 5th degree in x (years). The regression was not significant at any stage, nor were any of the terms significant. The quadratic term was negative and large enough to be suggestive, but even so accounted for a non-significant proportion of the variance. The sample of 14 years therefore did not provide any evidence of a long-term trend in the density of the population. It is therefore appropriate to conclude that the maximum annual density attained by the population had neither been increasing nor decreasing during the 14 years represented in this sample. Since four quantities derived entirely from meteorological records had accounted for 78% of the variance this may only be an indirect way of showing that there had not been a trend with time in those particular components of the weather.

(d) *The 'balance' of the population*

The theory of the 'balance' of animal populations rests largely on experimental results got from populations growing in artificial environments in laboratories (Pearl, 1926; Chapman, 1928; Holdaway, 1932); or on hypothetical mathematical models (Nicholson, 1933; Nicholson & Bailey, 1935). The theory states that 'balance' may be maintained only by the operation of 'density-dependent' components of the environment, since these alone fulfil the requirements of 'competition'. Without 'competition' (brought about by the operation of components whose influence varies in proportion to the density of the population) an increasing population would ultimately become infinitely large and a decreasing

population would ultimately become infinitesimally small and presumably become extinct. Since populations do not usually do either one or the other it is argued that all populations are in a state of 'balance' brought about by the operation of 'density-dependent' components in the environment.

An experimental population of host and predator living in an artificial environment which had been arranged to comply as nearly as possible with the requirements assumed for their mathematical models by Nicholson & Bailey, gave results during seven generations which closely approximated to those predicted by the theory (De Bach & Smith, 1941). The growth of the sheep population of South Australia followed a course which was consistent with the theory that 'density-dependent' components were of chief importance (Davidson, 1938). But the sheep also were living in an 'artificial' environment since it was to the farmer's advantage to maintain their population at the highest density consonant with a healthy development of the pastures. In the rather more 'natural' environments used by Gause and his associates to study the interaction of predator and prey, 'balance' was found to occur in two special cases where there was periodic immigration of hosts from a 'predator-free' reserve of hosts. In other cases the state of 'balance' did not develop: in some instances the predator died out while the host was still numerous, in others the predator first destroyed the host and then died out completely itself (Gause, Smaragdova & Witt, 1936). When we turn to the facts established by the present study of a natural population of *T. imaginis* we find that they are not altogether consistent with the theory as it stands at present.

Like many, if not most, insect populations in temperate climates the population of *T. imaginis* changed continuously and rhythmically with the changing seasons of the year (Davidson & Andrewartha, 1948). Each year about August it reached its lowest level: during the next 3 months the population grew rapidly reaching a maximum about the end of November, often at this time being several hundredfold more numerous than during August. During December the numbers declined abruptly and usually had reached a low level by January or February. Occasionally a slight temporary increase occurred during May–June, but in general the numbers continued to decline until August. This cycle was repeated with minor variations each year.

Since the population increased each year to a maximum and then declined, and since the size of the maximum attained each year showed no systematic trend with time it is relevant to ask: (*a*) what were the components of the environment which limited (or controlled) the growth of the population; and (*b*) was the population in a state of 'balance' with these components of the environment? If not there seems to be no sense in which the conception of balance may be applied to the observed fluctuations in the population at this time of the year.

This is indeed the central theme of the present paper. It has been shown that the maximum density attained by the population each year was related very closely to fluctuations in the weather during the preceding months. Four quantities derived entirely from meteorological records accounted for the major part of the annual variability in the thrips population. There was no evidence that the influence of these components of the environment varied with the density of the population, nor would one expect it to do so.

That four 'density-independent' components of the environment should have accounted for 78% of the variance of the population density ceases to be surprising when it is considered that the population did not normally attain anything like the density required to saturate the environment. On the contrary, during the favourable period for multiplication the number of flowers suitable for the breeding of *T. imaginis* increased enormously and usually very rapidly; and the density of the population relative to the available situations was so low that 'competition' was likely to be quite unimportant. The 'balance' (if that be a suitable term) is seen as a race against time; multiplication proceeded further and the population attained a greater density on those occasions when the favourable period was prolonged; multiplication was curtailed and the maximum density attained was lower when the favourable period was shorter. But on the average the physical environment remained favourable for far too short a period to permit the insects to multiply to a point where competition became important.

Nicholson & Bailey (1935) may have imagined such a situation when they wrote (p. 553): 'Moreover the competition which exists between searching animals is shown to produce certain effects such as balance and interspecific oscillation, which are independent of other environmental factors in their essential features and so must exist—unless the fundamental hypotheses given are wrong, or there is some factor capable of nullifying the effects of competition, which seems most improbable.' Experience suggests that the phenomenon which has been shown for *T. imaginis* to be 'capable of nullifying the effects of competition' may be quite commonplace, at least with species which live in temperate climates.

The theory of the balance of animal populations postulates the operation of 'density-dependent' components in the environment of a decreasing population. Otherwise the population would become infinitesimally small and die out. (Nicholson, 1933, p. 136). The population of *T. imaginis* was usually decreasing during the period December to August each year.

The mortality which occurred each year during the summer was tremendous. During the spring fields, gardens, headlands, roadsides, indeed the whole countryside may harbour flowering plants which may provide favourable situations for *T. imaginis*. During the summer these disappeared and the insects died out completely from the greater part of the terrain which they had previously occupied. The survivors were to be found in restricted local situations scattered thinly throughout the area of 'permanent' distribution of the species. The garden at the Waite Institute where our records were taken represented one such situation. Since the mortality each year was tremendous, yet never proceeded to the point where the species died out completely, it is relevant to ask: (*a*) what were the components of the environment which controlled the density of the population at this time of the year; and (*b*) was the population in a state of 'balance' with these components of the environment?

No attempt has been made to relate the minimum numbers observed to any selected components of the environment in the same way that the maximum density was studied. But observation indicates that predators, parasites and disease played a negligible part in controlling the population. Nor was there any evidence of intraspecific competition, since at this time of the year the flowers always contained far fewer thrips than the maximum they could support.

In the absence of precise statistical measurement the components of the environment which may be associated with the minimum density of the population may only be guessed at. But it would be a mistake to suppose that the components of the physical environment (e.g. summer drought) operate at an intensity which is independent of the density of the population. This becomes clear when the detailed geographic distribution of the insect is considered.

The geographic distribution of *T. imaginis* has not been studied in detail. But for the springtail, *Smynthurus viridis*, Davidson (1934) showed that there was a close relationship between the distribution of the insect and the distribution of certain climatic zones. He mapped four zones of decreasing degrees of favourableness. Outside the least favourable zone the insect was unable to survive the unfavourable season of the year even in the most favourable situations. Inside the most favourable zone no conceivable variation in the weather could destroy all the insects in the more favourable situations. A detailed study of the ecology of the grasshopper, *Austroicetes cruciata*, established the same principles. During the years 1936 and 1937 the insects colonized a large area in western Australia which was outside the zone where swarms normally occur. With the return of more 'normal' weather in 1938 the insects died out of this area but persisted in the zone of 'permanent' distribution (Andrewartha, 1944). In the 'grasshopper belt' of South Australia *A. cruciata* is able to increase in numbers during a number of years and then a drought may cause a 'crash'. The insect may die out completely from all but a few local situations. The complete annihilation of the grasshopper during a drought is prevented by the existence of scattered niches, be they ever so small, where some food remains (Andrewartha & Birch, 1948).

Similarly *Thrips imaginis* was reduced each year during the unfavourable season to local situations which were more favourable than the surrounding countryside. Some of these situations may be 'marginal' in that some thrips may survive in them some years. Outside the area of 'permanent' distribution of the species there may be some situations where some individuals may survive in some years but die out completely in other years. Inside the zone of permanent distribution there are some situations so favourable that no conceivable variation of weather will destroy all the insects in them. These local situations may be arranged in a graded series from the most favourable through the marginal down to those so unfavourable that all the insects will disappear from them during the unfavourable season every year.

At the end of spring most of the population occurred in situations which readily became unfavourable with the approach of summer. Thus, while the population was large, a small increase in the severity of the weather destroyed a large proportion of the population. As the numbers were reduced the insects were restricted to an increasing extent to the more favourable situations and relatively large increases in the severity of the weather destroyed relatively fewer of the total population. Indeed no conceivable variation in the weather is likely to destroy all the insects in these situations in the time available: by the time spring comes the population ceases to decline and begins to increase once again in response to the changing physical environment.

In this special sense the physical environment (as determined by the weather) becomes one of the 'density-dependent' components of the environment, and the facts observed with *T. imaginis* during the period of the year when the population was declining can be fitted into the general theory. But this interpretation requires a restatement of the theory with respect to detail since Nicholson (1933, pp. 135–6) clearly excludes climate from the list of possible 'density-dependent factors'.

8. SUMMARY

1. Daily counts of the numbers of *Thrips imaginis* in roses in the garden at the Waite Institute have been made continuously for 14 years. The roses used for sampling were highly attractive to the adult thrips

but were not favourable for the development of immature stages. They served as a 'trap' which gave a satisfactory indication of the density of the population in the area.

2. The method of partial regression was used to measure the degree of association between the numbers of thrips present during the spring and the weather experienced during the preceding months.

3. With the aid of precise knowledge of the biology of *T. imaginis* and the weather of the Adelaide area it was possible to select four components of the physical environment which were likely to be closely associated with the density of the thrips population in the spring. The analysis showed that 78 % of the variance of the population could be related to these four quantities.

4. The maximum density attained by the population in the spring is largely determined by the weather during the preceding autumn, but rainfall and temperature during the early spring may modify the tendencies established in the autumn.

5. 'Competition' plays little or no part in determining the maximum density attained in the spring. Rapid multiplication is possible only for a limited period during spring and early summer. During this period the insects increase rapidly but so does the number of situations available to them; and the favourable period normally ends long before the thrips have had time to saturate the environment. The onset of summer drought brings about a 'crash' and the numbers decline to the low level characteristic of late summer and winter. The 'balance' of the population is seen as a race against time with the increase in density being carried further in those years when the favourable period lasts longer, but never reaching the point where competition begins to be important. The annual fluctuations in the maximum density attained by the population are controlled almost entirely by 'density-independent' components of the environment.

6. During the period each year when the population is decreasing weather is still the most important influence at work to determine the density of the population. The population never decreases to zero, partly because during this phase of the 'population rhythm' weather operates as a 'density-dependent' component of the environment, and partly because the spring supervenes and the population begins increasing under the influence of the changing environment.

7. It was also shown in the earlier part of the paper that the movement of the thrips into the flowers is influenced by the daily weather. The movement was greater during warm dry days and less during cold wet ones.

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THE ECOLOGY OF THE LOUGH INE RAPIDS WITH SPECIAL REFERENCE TO WATER CURRENTS

2. THE FAUNA OF THE *SACCORHIZA* CANOPY*

By F. J. EBLING, J. A. KITCHING, R. D. PURCHON† and R. BASSINDALE

From the Department of Zoology, University of Bristol

(With Plate 4, and 14 Figures in the Text)

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1. INTRODUCTION

Lough Ine (Co. Cork, Eire) is a marine lough connected with the sea by a narrow channel known as the Rapids, through which sea water flows in and out with great force under the influence of the tide. The general features and hydrography of the Rapids have already been described in the first paper of this series (Bassindale, Ebling, Kitching & Purchon, 1948). The Rapids constitute a natural experiment for the investigation of the effect of current on marine sublittoral organisms, since within a short distance currents range from 3 m./sec., attained on the Sill, to practically still water such as is found in the Lough above the Rapids and in Barloge Creek below them.

Whereas the current is the most obvious and probably by far the most important variable in the Rapids area, it is not possible to exclude entirely other factors, such as sedimentation, which are partially dependent on it. The same sea water flows all through the Rapids, so that there is obviously a strong tendency for any variations of salinity, oxygen tension and so forth to affect all parts equally. Nevertheless, in places where the water is very quiet, or circulates in an eddy, differences may be set up. This is certainly true in the case of water temperature, as is shown in the records already given (Bassindale *et al.* 1948).

The bottom of the Rapids is rocky or strewn with boulders, and is covered with laminarian algae, of which *Saccorhiza bulbosa* de la Pyl (Newton, 1931)—also commonly known as *S. polyschides* Batt—is by far the most plentiful. The fronds of *Saccorhiza* stream out in the current and form a canopy which completely hides the bottom. The organisms living on the fronds are therefore likely to be more exposed to the current than those on the underlying boulders. For this reason the canopy with its population forms a natural starting-point for the biological side of the present investigation.

The work described in this paper comprises an investigation of the current immediately above the canopy of *Saccorhiza* fronds at a series of stations in the Rapids area, and an investigation of the fauna of the canopy at these stations.

This work has been carried out by three expeditions‡ (July 1938, September 1946 and July 1947) from the Department of Zoology of the University of

* Part 1, 'Introduction and hydrography', is appearing in the *Journal of Ecology*.

† Now at the Department of Zoology, University College, Cardiff.

‡ The following took part as students in the field work described in this paper: in 1938, S. Bennett, Jean M. Fry, H. Gorvett, J. S. Hellier, D. A. Parry, Ruth Parry, H. F. Steedman, Nita Wigmore; in 1946, Avice Brindley (St Andrews), Betty W. Knight, Sylvia J. Lilly, Constance Plaice, Patricia E. Wade; in 1947, Mary Day, Estelle Davies, J. B. Gilpin Brown, Mary Harrison, Mary Hay, D. Johns, Sylvia J. Lilly, Elizabeth Manners, Margaret Manning, Rachel Noble, Constance Plaice. Catering was carried out by Phyllis Whitton in 1946 and by Diana Purchon in 1947.

Bristol to the University of Cork's marine biological station at Lough Ine.

2. WATER CURRENTS

A detailed investigation of water current was made at a series of stations in the Rapids area, most of them being along the west bank. The positions of these stations are shown in the map in Fig. 1. Usually the current was measured with a Watts meter as already described (Bassindale *et al.* 1948), except that the pole carrying the meter was held from the quay or shore. The bottom of the pole was thrust firmly on to the sea bed after the meter had been adjusted to such a position on the pole as to bring it just above the canopy. Some of the readings taken at neap tides at stations of very low current were made with a more sensitive meter fitted with rotary vanes which had been constructed and lent to us by Dr H. W. Harvey of Plymouth. Readings were taken at intervals throughout the day at neap tides (13 July 1947 for west bank and 14 July 1947 for east bank) and at spring tides (20 July 1947 and a few readings on 19 July, west bank only). All readings were taken in duplicate, and agreement was excellent except at one station (J) where there was characteristically a considerable variability.

Fig. 1. Position of canopy stations. Note: stations B–E are about 1½ m. from the edge of the quay. The depth of the bottom at all stations is about 1 m. below the lowest level reached by the water at these stations at ordinary spring tides.

The results of this work are given in Fig. 2. As in the case of the longitudinal section of the Rapids, and for reasons already discussed (Bassindale *et al.* 1948) at stations below the Sill the fastest currents were experienced during outflow, whereas above the Sill they were experienced during inflow. For biological purposes it seems reasonable, in an attempt to summarize the characteristics of each station, to extract from Fig. 2 the maximal current and the total flow passing during a complete cycle of the tide (about 12½ hours) in each case. Since a station in the canopy may be regarded as a point, the total flow can conveniently be expressed in terms of the length of water passing, inflow and outflow being added together. This was estimated from the area enclosed within the current-time graph; smoothed curves were used because these seemed likely to provide better estimates. The results of this analysis are given in Table 1; essential features of the current at the level of the canopy are illustrated in the maps in Fig. 3. The strongest currents and greatest total flows are at stations E, F and G, on or near the Sill. Stations B, C, J and K, in the direct line of the current but some distance above and below the Sill, are moderate in respect of strength and total flow. The weakest current and the least flow are at A (in Renouf's Bay), L (Eddy Creek), and M (at the north end of Southern's Bay). We did not obtain any measurements of current at spring tides for stations N, P and R. Our experience in rowing at station P indicates that this may be classed as moderate in respect of current. Station R, though in the open channel, does not receive the full force of inflow owing to the recession of the east bank from the Sill northwards; from the data for neap tides it may be classed as a quiet water station verging towards moderate current. Station N, which is close to M in Southern's Bay, is obviously subject only to weak current. In general, those stations with high maximal currents have a high total flow, and those with low maximal currents have a low total flow. The few slight exceptions (compare stations B and C) to this rule unfortunately do not provide a sufficient basis for distinguishing between the effects of

Photo J. A. Kitching

A view of Lough Ine Rapids during outflow, looking north towards the Lough.

Table 1. *Currents at canopy stations* 1947

Station	Neap tide *		Spring tide	
	Total flow per tidal cycle (km.)	Maximal current (m./sec.)	Total flow per tidal cycle (km.)	Maximal current (m./sec.)
A	6	0·45	7	0·5
B	12	1·1	17	1·5
C	23	1·1	22	1·3
E	39	1·9	45	1·9
F	46	1·6	57	2·4
G	42	2·2	66	2·6
J	21	1·3	27	1·4*
K	16	0·6	31	1·0
L	0·4	0·09	6	0·6
M	<0·3	0·09	5	0·3
N	<0·3	<0·01	.	.
P	13	0·6	.	.
R	7	0·3	.	.

* Readings very variable.

maximal current and total flow on the animal population.

We hope on a future occasion to obtain data concerning the duration of slack water and of conditions of low current at each station, since these are likely to be important in connexion with the settling of larvae.

3. OBSERVATIONS ON THE FAUNA OF THE CANOPY

(*a*) *Introductory survey of the fauna*

The large brown 'oar-weed' *S. bulbosa* (Fig. 4) consists of a bulbous holdfast, a flat strap-like stipe, and a wide blade-like frond which is often cleft radially into a number of strips. The margins of the lower part of the stipe are expanded and crenulated, and are hereafter referred to as the 'frills', in contrast to the flat surfaces of the stipe or 'flats'. Many *Saccorhiza* were found of from 2 to 3 m. in length, and several of over $3\frac{1}{2}$ m.

A characteristic fauna and flora is found on *S. bulbosa* in the Rapids area, and there are considerable differences between the populations of the various parts of the alga. The flora of epiphytic algae, described by Rees (1931), includes the filamentous forms *Litosiphon* spp. and *Polysiphonia* spp. A brief survey of the more important components of the fauna, as seen by us, is now given in order to make it easier to understand the account of our work which follows. The fauna of the holdfasts does not fall within the scope of this paper.

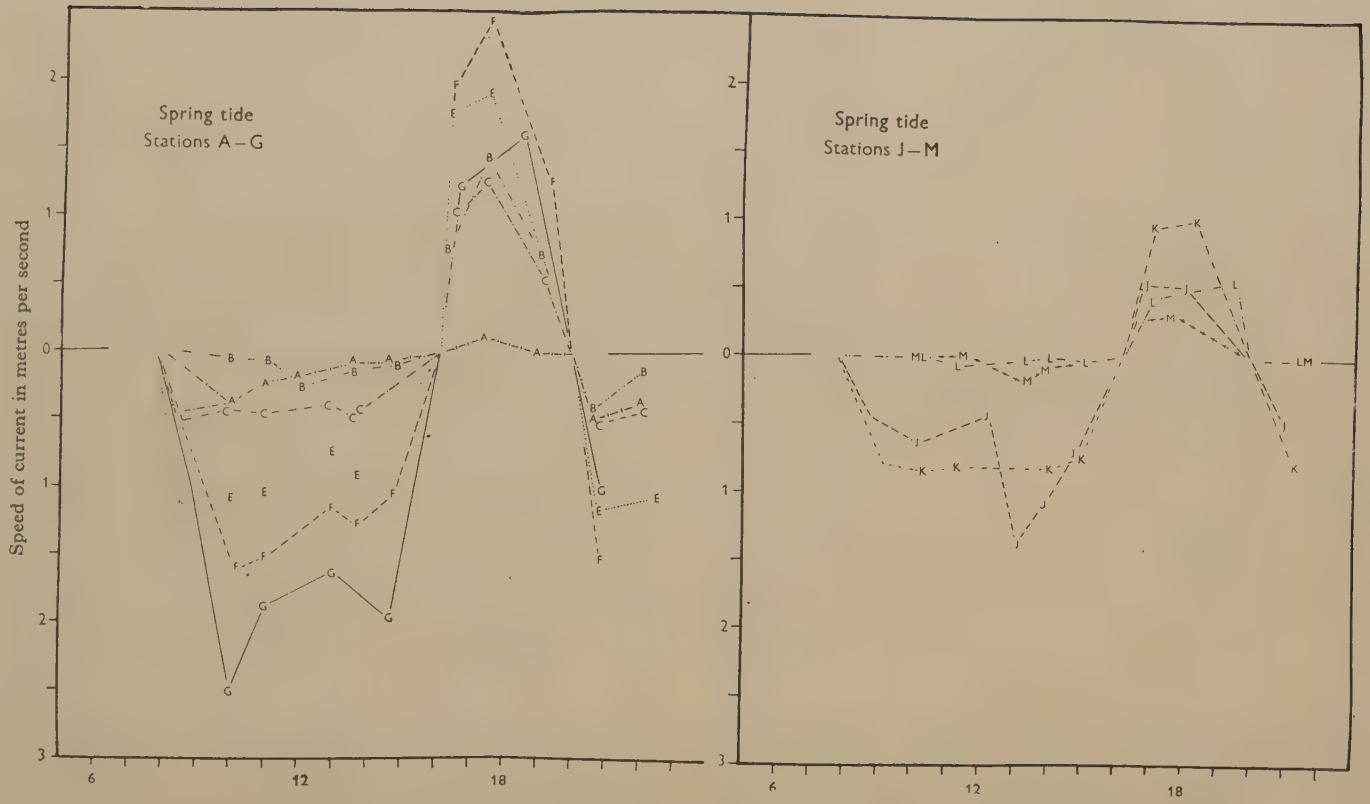
Many animals are found permanently attached to the fronds and stipes of *Saccorhiza* in the Rapids area. These include Polyzoa, colonial tunicates, and hydroids. The encrusting polyzoan *Membranipora membranacea* spreads in white sheets over fronds and stipes and sometimes almost completely covers them. Another encrusting polyzoan, *Hippothoa* (*Schizoporella*) *hyalina*, grows as numerous small patches closely pressed to the surface of its seaweed substrate. Two other common Polyzoa are *Scrupocellaria reptans*, a tufted and branched form, and *Tubulipora plumosa*, which forms small compact erect colonies. The hydroid *Obelia geniculata* is locally plentiful on both fronds and stipes, while another hydroid, *Tubularia bellis*, was unusually abundant in July 1947 on the frills. The tube-worm *Spirorbis* sp. is locally abundant on the fronds of *Saccorhiza*.

Chief among motile species associated with *S. bulbosa* are a number of gastropod molluscs, including especially *Gibbula cineraria* and the small limpet *Patina pellucida*. The latter eats shallow depressions in the surface of the *Saccorhiza*. In certain places the frills hold great numbers of the tubes of the amphipod *Jassa falcata*. Very many other motile forms are found less frequently (see Table 3).

As it was our aim to study the distribution of a limited number of common species carefully, rather than to list the complete fauna, lack of mention of some species does not necessarily imply that they did not occur. As our time was limited we were for instance obliged to ignore certain amphipods, tunicates, and sponges which we could not identify safely in the field. We hope, however, that the number of species studied will prove sufficient to establish certain principles regarding the effects of current on sublittoral animals.

(*b*) *Methods of assessment of population density*

The abundance of various animals associated with *Saccorhiza* was estimated approximately both by


Spring tide
Stations A – G
Spring tide
Stations J – M
Speed of current in metres per second
0
1
2
3
6
12
18

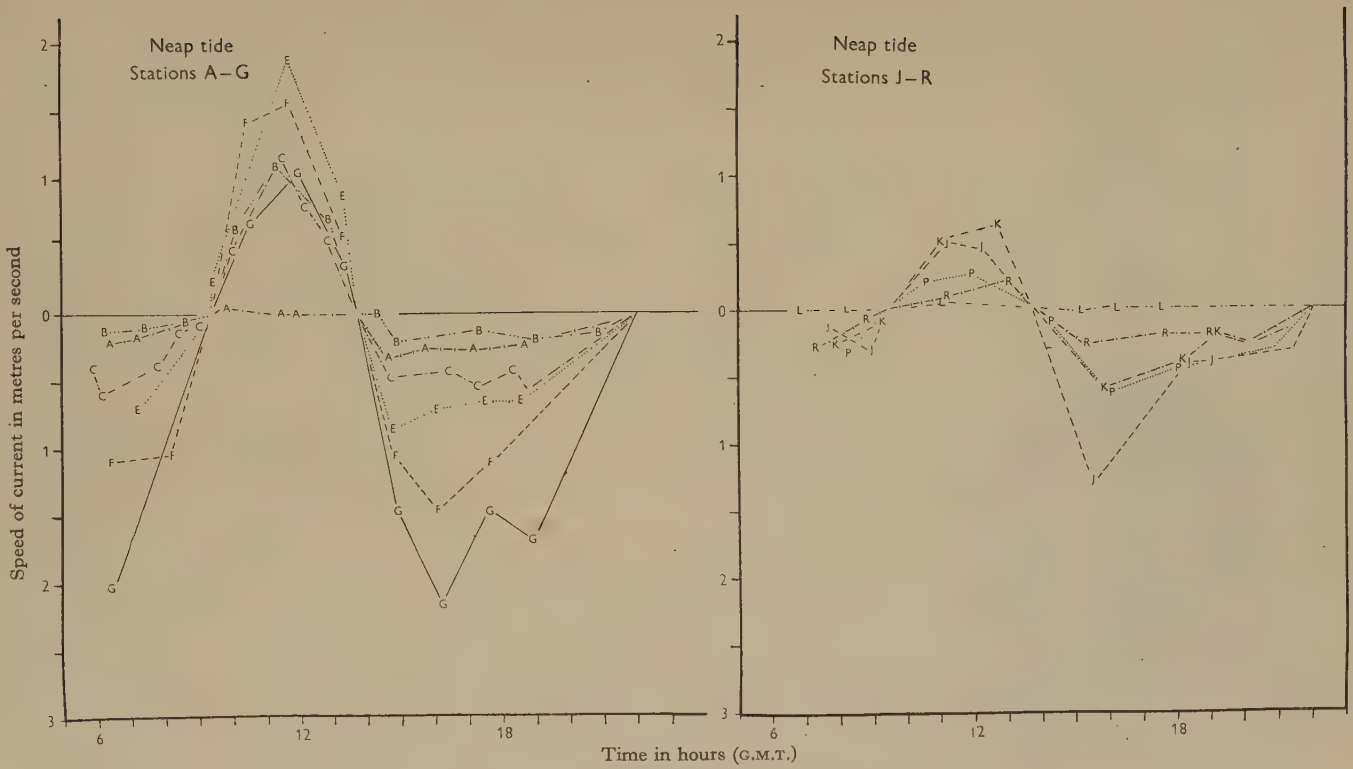


Fig. 2. Speed of current at canopy stations throughout spring and neap tidal cycles. Readings were taken just above the canopy. Data are only available for the stations listed in Table 1.

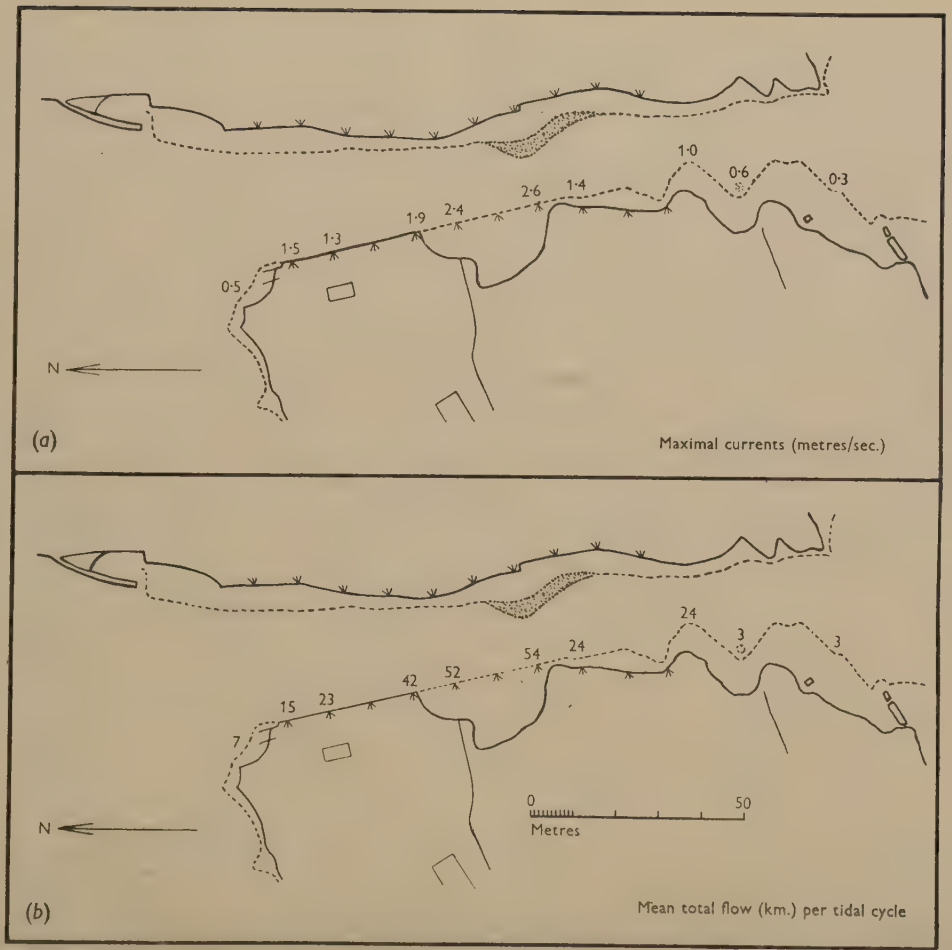


Fig. 3. Certain essential features of water currents at level of the canopy. (*a*) Maximal currents in metres per second. (*b*) Mean total flow in kilometres per tidal cycle (based on average of figures for spring and neap tides).

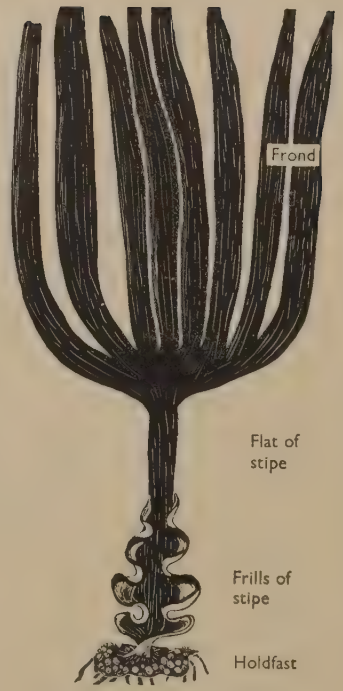


Fig. 4. *Saccorhiza bulbosa.*

subjective impressions of one or more observers and by counts from samples. Subjective impressions were recorded by the following symbols: ○ means 'absent (in so far as the observer could determine)'; ◔ means 'one or a few only were seen'; ◐ means 'moderate in quantity'; ● means 'plentiful (i.e. of the same order of abundance as the greatest known to us in Lough Ine, the Rapids or Barloge Creek)'.

(c) *Observations*

Preliminary work was done in July 1938. This included a general survey of *Saccorhiza* plants collected throughout the Rapids area and a detailed examination of a number of fronds and stipes collected from Eddy Creek (quiet water), from the east side opposite point 3 (moderate current), and from the Sill (strong current). The results are in general agreement with those obtained later and therefore are not presented here.

A survey was made in September 1946 of the distribution of the encrusting polyzoan *Membranipora membranacea* and the gastropod *Gibbula cineraria* on the fronds of *Saccorhiza* (and—on the Sill—of *Laminaria digitata*) throughout the Rapids area. Two observers worked together from a boat and from the shore. The population density of *Membranipora membranacea* was expressed as the estimated percentage of the visible area of fronds covered with this polyzoan. The observations recorded in Fig. 5 were all made during outflow of the Rapids. (A smaller number of estimates made during inflow failed to reveal any significant differences from those taken during outflow at the same positions.) Estimates of the population density of *Gibbula cineraria* were also subjective and were recorded by means of symbols. The results are given in Fig. 10.

A quantitative comparison was made in September 1946 of the fauna on *Saccorhiza* plants collected from a series of stations (Fig. 1) throughout the Rapids area. Four plants were collected at each station; subsequently additional plants (usually four) were collected at each station and examined for *Patina* only, as the first results appeared to indicate a need of additional information. The results are summarized in Tables 2 and 3, and (in the case of *Patina*) in Table 4; they are illustrated in Figs. 5–12 and in Fig. 14.

A further investigation of the distribution of *Patina*

Fig. 5. Distribution of *Membranipora membranacea*, on fronds of *Saccorhiza bulbosa*, expressed as a percentage of total visible area of weed covered, as estimated from shore or boat. Current flowing out. September 1946.

was made in July 1947 on samples of *Saccorhiza* collected for biometric studies. Over 100 plants were examined for *Patina*, and the data for fronds, flats of stipes, frills of stipes, and holdfasts were kept separately. The results of this study are summarized in Table 5 and Fig. 13.

(d) *Analysis of results*

(1) *Animals permanently attached to* Saccorhiza

Membranipora membranacea (Polyzoa) (Figs. 5 and 6) was scarce or absent on all parts of *Saccorhiza bulbosa* in quiet water (stations A, L, M). It was found on all parts of *Saccorhiza* growing in moderate current (stations B, C, J, K, P, R), where it was very abundant on the fronds. It was absent from the

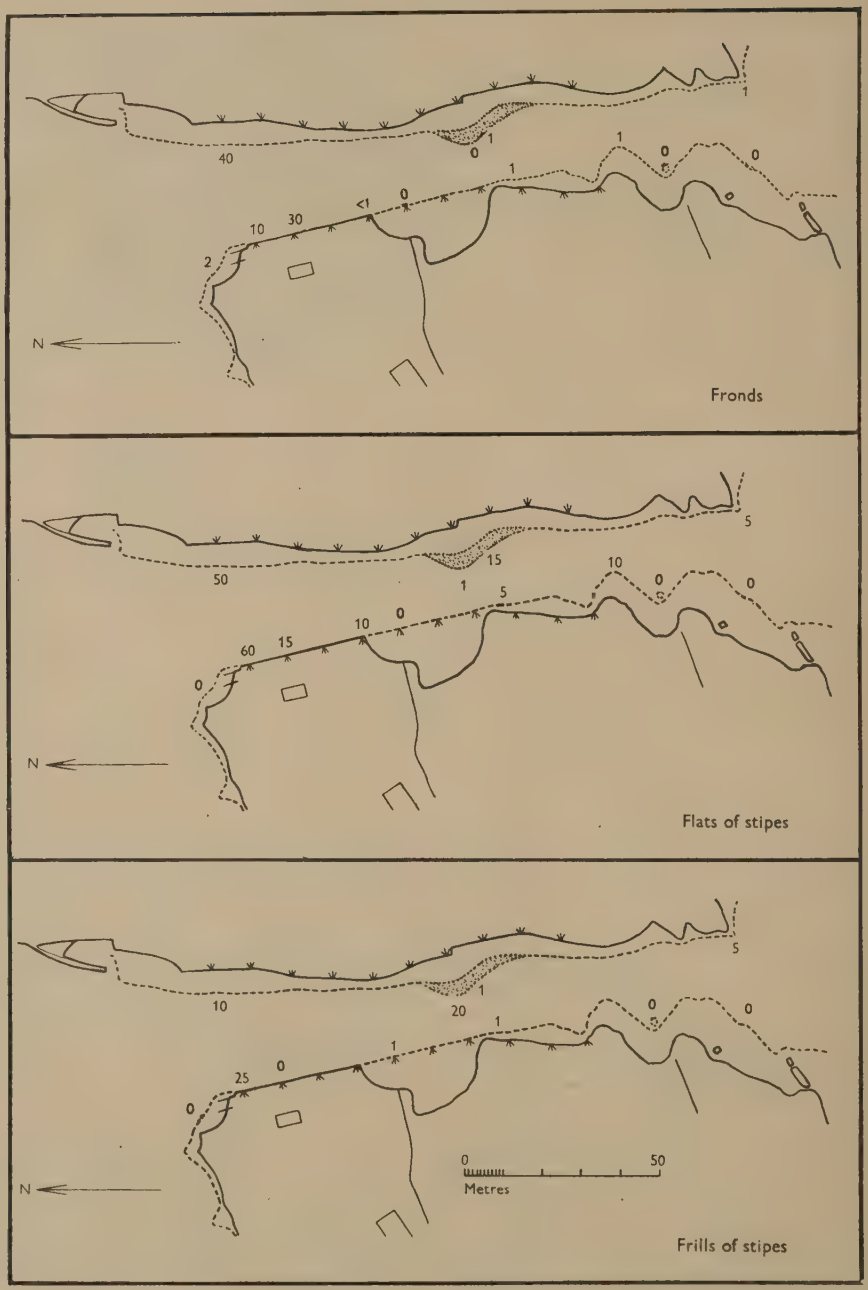


Fig. 6. Percentage of surface area of fronds, flats of stipes, and frills of *Saccorhiza bulbosa* covered by *Membranipora membranacea* in September 1946, as determined by estimation from samples (Table 2).

Table 2. *Distribution of commoner species found on* Saccorhiza bulbosa *(excluding holdfasts), September* 1946

Species	Station A				Station B				Station C			
Anomiid spat												
Frond	.	300	700	2000	.	.	.	.	1	.	.	.
Stipe	.	80	9	.	.	.	.	.	.	.	1	.
Frills	*	.	.	.	.	.	.	.	63	100	.	58
Tubulipora plumosa Thom.												
Frond	2	32	4	155	.	.	.	.	.	.	.	.
Stipe	1	8	7	.	.	.	.	.	2	.	.	8
Frills	.	4	4	4	.	13	13	11	21	100	137	47
Membranipora membranacea (L.)												
Frond	1	.	7	1	5	5	30	10	15	15	45	40
Stipe	.	.	.	.	20	90	90	40	20	15	5	25
Frills	.	.	.	.	5	5	5	90	.	.	.	.
Patina pellucida (L.)												
Frond	2	2	7	1	13	26	37	25	13*	9	11	9
Stipe	.	.	.	.	.	2	3	1	.	.	3	.
Frills	.	.	.	1	.	6	21	2	30	24	7	24
Hippothoa hyalina (L.)												
Frond	.	700	500	1000	.	.	.	.	.	3	.	.
Stipe	9	61	21	.	.	.	.	.	.	.	.	5
Frills	.	22	6	38	2	1	500	.	44	100	60	46

Species	Station E				Station F				Station H				
Anomiid spat													
Frond	.	.	.	.	.	.	.	.	.	.	.	.	.
Stipe	.	.	.	.	.	.	.	.	.	.	.	.	.
Frills	4	1	.	11	.	.	.	.	.	.	8	.	.
Tubulipora plumosa Thom.													
Frond	.	.	.	.	.	.	.	.	.	.	.	.	.
Stipe	.	.	.	.	.	.	.	.	.	.	.	.	.
Frills	5	6	22	28	.	6	38	20	.	.	11	4	.
Membranipora membranacea (L.)													
Frond	1	.	.	.	.	.	.	.	.	.	.	.	.
Stipe	5	15	15	5	.	.	.	.	5	.	.	.	.
Frills	?	?	?	?	1	1	.	1	60	.	.	1	20	50
Patina pellucida (L.)													
Frond	11	2	1	8	7	2	8	3	1	2	1	2	.	.	.
Stipe	2	.	.	.	2	.	.	.	.	1	2	2	.	.	.
Frills	13	5	4	2	2	.	.	5	1	6	2	1	4	1	.
Hippothoa hyalina (L.)													
Frond	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Stipe	.	1	.	.	.	.	.	.	.	.	.	.	3	.
Frills	3	13	50	24	.	25	1	30	.	.	1	.	41	.	.

Species	Station J				Station K				Station L			
Anomiid spat												
Frond	.	.	.	.	.	.	.	.	.	.	.	.
Stipe	.	.	.	.	.	.	.	.	.	.	.	.
Frills	.	.	7	2	2	50	2	2	.	.	.	.
Tubulipora plumosa Thom.												
Frond	.	.	.	.	.	.	.	.	.	.	.	.
Stipe	.	.	.	.	.	.	.	.	.	7	3	1
Frills	.	18	29	2	10	23	8	52	2	7	5	4
Membranipora membranacea (L.)												
Frond	.	1	1	.	1	3	1	5	.	.	.	.
Stipe	.	10	1	2	2	5	15	15	.	.	.	.
Frills	.	.	1	1	.	?	.	?	.	.	.	.
Patina pellucida (L.)												
Frond	17	62	35	3	22	18	40	3	7	1	6	1
Stipe	1	2	3	3	1	.	.	.	2	.	.	.
Frills	.	18	15	3	3	2	9	6	1	.	.	.
Hippothoa hyalina (L.)												
Frond	.	.	.	.	.	.	.	.	60	160	1000	90
Stipe	.	.	72	.	.	.	.	.	20	26	45	118
Frills	1	100	137	15	5	180	9	80	*	2	5	5

Table 2 (*continued*)

	Station M				Station R			
Anomiid spat								
Frond	1000	2000	900	1500	3	14	9	65
Stipe	120	*	70	140	2	3	3	7
Frills	.	*	30	200	1000	200	1000	1000
Tubulipora plumosa Thom.								
Frond	113	86	250	300	4	1	4	9
Stipe	14	10	27	80	.	.	.	.
Frills	28	18	44	110	30	66	60	10
Membranipora membranacea (L.)								
Frond	.	.	.	.	20	45	60	30
Stipe	.	.	.	.	60	40	20	70
Frills	.	.	.	.	10	10	5	5
Patina pellucida (L.)								
Frond	6	4	2	2	7	12	8	8
Stipe	.	.	.	.	1	.	1	.
Frills	1	1	.	1	1	7	6	1
Hippothoa hyalina (L.)								
Frond	200	600	400	750	184	179	105	460
Stipe	200	110	210	140	7	2	29	22
Frills	30	12	130	150	600	1000	1000	1000

	Station Q				Station P			
Anomiid spat								
Frond	.	.	.	.	.	.	.	1
Stipe	.	.	.	.	2	.	.	.
Frills	.	25	5	.	300	166	130	.
Tubulipora plumosa Thom.								
Frond	.	.	.	.	.	.	.	.
Stipe	.	.	.	.	1	.	.	.
Frills	15	12	56	22	31	17	2	.
Membranipora membranacea (L.)								
Frond	1	1	1	1	2	1	1	.
Stipe	.	20	20	20	1	.	25	.
Frills	.	.	5	.	.	.	10	.
Patina pellucida (L.)								
Frond	9	15	.	18	20	48	30	24
Stipe	1	.	1	.	.	.	4	2
Frills	16	20	14	14	7	11	10	8
Hippothoa hyalina (L.)								
Frond	.	.	7	.	.	.	.	.
Stipe	15	6	3	6	28	8	.	.
Frills	1000	258	1000	205	1113	1000	75	.

* A few.

Note. Anomiid spat and *Patina* are given as the number of individuals, *Tubulipora* and *Hippothoa* as the number of colonies, and *Membranipora* in terms of the estimated percentage area of plant surface covered. Round numbers, e.g. 100, 200, etc., were chiefly obtained by estimation, either by comparison with a control sample, or from a count of a part of the population. *Jassa falcata* (Mont.) was found in abundance at some stations, but was only estimated subjectively. Its distribution is shown in Fig. 12.

Table 3. *Distribution of less common species found on* Saccorhiza bulbosa *(excluding holdfasts), September* 1946

+ Indicates the occurrence of a species

Station	A	B	C	E	F	H	J	K	L	M	R	Q	P
Tubularia bellis Allman	.	+	.	.	.	+	.	.	.	.	.	+	+
Obelia geniculata L.	+	.	+	.	.	+	+	.	.	.	+	+	+
Corynactis viridis Allman	.	.	.	.	.	.	.	.	.	.	.	+	.
Pomatoceros triqueter (L.)	.	.	.	.	.	.	.	.	.	+	.	+	+
Spirorbis sp.	+	.	.	.	.	.	.	.	.	+	.	.	.
Carcinus maenas Pennant	.	.	+	.	.	.	.	.	.	.	.	.	.
Galathea squamifera Leach	.	.	.	.	.	.	.	.	.	.	.	+	+
Pycnogonid	.	.	.	.	.	.	.	+	.	+	.	.	.
Mytilus edulis L.	.	.	+	+	.	+	+	.	.	+	.	.	.
Musculus marmoratus (Forbes)	+	.	.	.	.	.	.	.	.	+	.	.	.
Hiatella arctica (L.)	.	.	+	+	.	.	.	.	.	+	+	.	+
Spat: *Pecten maximus* (L.) / *Chlamys opercularis* (L.)	+	.	.	.	.	.	.	.	.	+	+	.	.
Gibbula cineraria (L.)	+	+	.	+	+	+	+	+	.	+	.	+	.
Calliostoma zizyphinum (L.)	.	+	.	+	.	.	.	.	.	+	.	+	.
Lacuna vincta (Montagu)	+	.	.	.	.	.	.	.	.	+	.	.	.
Littorina littoralis (L.)	.	.	.	+	.	.	.	.	.	+	.	.	.
Barleeia unifasciata (Montagu) (=*Rissoa rubra*)	.	.	.	.	.	.	.	.	.	.	+	.	.
Trivia monacha (da Costa)	.	+	.	+	.	.	.	.	.	.	.	.	.
Bittium reticulatum (da Costa)	+	.	.	.	.	.	.	.	+	+	+	.	.
Nassarius incrassatus (Ström)	+	.	.	.	.	.	.	.	.	.	.	.	.
Polycera quadrilineata (O. F. Müller)	.	.	.	.	.	+	.	.	.	.	.	.	.
Scrupocellaria reptans (L.)	+	.	+	.	.	.	.	.	.	+	.	.	+
Asterina gibbosa (Pennant)	+	.	.	.	.	.	.	.	.	+	.	.	.
Ophiuroids	+	.	.	+	.	+	+	.	.	+	+	.	.

Table 4. *Population of* Patina pellucida *on* Saccorhiza bulbosa (*fronds and stipes inclusive*)

Station	No. of *Saccorhiza* collected	Mean wt. of *Saccorhiza* (and range) in lb.	Mean no. of *Patina* per *Saccorhiza*	Standard error to mean in preceding column	No. of *Patina* per 3 lb. of *Saccorhiza* collected
A	4	3·6 (1·0–9·8)	3·3	1·4	2·7
B	8	3·7 (1·0–9·5)	22·0	6·6	17·8
C	8	4·1 (1·8–6·3)	34·4	3·3	25·6
E	8	3·3 (1·3–5·5)	10·9	3·2	9·7
F	8	2·8 (2·0–4·5)	8·0	1·0	8·5
H	7	1·3 (0·8–2·5)	4·0	1·1	9·3
J	8	2·9 (1·3–4·8)	33·4	10·6	34·4
K	9	2·8 (1·3–4·5)	30·8	8·6	31·9
L	8	2·5 (0·8–6·8)	14·1	6·7	17·2
N	8	2·8 (1·0–4·8)	3·0	1·1	3·2

Table 5. Patina pellucida *on* Saccorhiza bulbosa. *Summary of collections made in July* 1947

Station	A	M	C	E
Numbers of plants collected	5	20	40	53
Total weight of fronds (kg.)	3·2	15·8	31·6	36·9
Total weight of stipes (kg.)	2·0	7·9	30·2	34·9
Total weight of holdfasts* (kg.)	—	1·5	3·2	5·6
Total number of *Patina* on fronds	5	23	1040	490
Average number of *Patina* per frond	1·0	1·2	26·0	9·2
Average number of *Patina* per kg. of fronds	1·6	1·5	32·9	13·3
Total number of *Patina* on stipes	0	9	279	177
Average number of *Patina* per stipe	0	0·5	7·0	3·3
Average number of *Patina* per kg. of stipe	0	1·1	9·3	5·1
Total number of *Patina* on flats	0	4	32	48
Total number of *Patina* on frills	0	5	247	129
Total number of *Patina* on holdfasts*	0	0	7	2

* A few holdfasts were lost during the process of collection, but the results are not likely to have been affected significantly.

fronds in strong current (stations E, F, H), but persisted on the frills. This statement is based not only on the results of the 1946 survey (Table 2), but on general observations carried out in 1938, when this same conclusion was reached. The restriction of this species to the frills in places of fast current strongly supports the view that the distribution of *Membranipora membranacea* over the Rapids area is primarily determined by current. A similar phenomenon is found for the next two species of Polyzoa and the same interpretation applies.

Hippothoa hyalina (*Schizoporella hyalina* in Plymouth List) (Fig. 7), also an encrusting form, was abundant on the fronds of *Saccorhiza* in Renouf's Bay, in Eddy Creek, and off Nita's Rock—all of these stations being in quiet water. It was practically confined to the frills in places where the current was strong or even moderate. This conclusion is based on quantitative estimates made in 1946 and on the general observations of 1938.

Tubulipora plumosa (Fig. 8) was also abundant on the fronds of *Saccorhiza* in Renouf's Bay and off Nita's Rock (both in very quiet water), and was present on fronds south of the Harbour at station R. It was not found on the fronds at any other station, but was found on the frills at all stations.

Anomiid spat (Lamellibranchiata) (Fig. 9) was found in September 1946 attached to the fronds of *Saccorhiza* in large numbers in Renouf's Bay and off Nita's Rock, and to a lesser extent south of the Harbour (at station R). At stations of greater current it was confined to the frills.

Scrupocellaria reptans (Polyzoa) and *Spirorbis* sp. (Polychaeta) were recorded from *Saccorhiza* only in Renouf's Bay and off Nita's Rock (September 1946).

Various compound ascidians were found on the fronds of *Saccorhiza* in Renouf's Bay (station A), off Nita's Rock (station M), and south of the Harbour (station R), but only on the frills (and occasionally on the flat parts of the stipes) elsewhere. *Tubularia bellis* was plentiful in those parts of the Rapids area where the current was strong or moderate (stations B, C, J and especially E), on the frills of *Saccorhiza*, in July 1947. It was absent on that occasion from *Saccorhiza* collected in Renouf's Bay, and little if any was present off Nita's Rock (station M).

(2) *Motile forms*

Jassa falcata (Amphipoda) (Fig. 12) was found in very large numbers in its tubes attached to the frills of *Saccorhiza*. It was abundant at all stations where the current is strong, occurred in small quantities in moderate current and was absent from all stations where the current is weak.

Gibbula cineraria (Gastropoda) (Fig. 10) was found occasionally throughout the Rapids area on the frills of the stipes of *Saccorhiza*. As observed from a boat, it was only present on the fronds of *Saccorhiza* in the quieter regions of the Rapids area, and in no part was it as abundant as near the southern end of Barloge Creek.

Bittium reticulatum (Gastropoda) (Fig. 11) was not found in very large numbers, but the records are sufficient to justify consideration. It was found in September 1946 on one or more of the *Saccorhiza* plants collected from Renouf's Bay, from station R (south of the Harbour), from Eddy Creek (station L) and from near Nita's Rock (station M)—all stations of weak current—but was not found on *Saccorhiza* from any other part of the Rapids area.

Rissoa parva (Gastropoda) was also collected on *Saccorhiza* but only in relatively small numbers. It was found most plentifully off Nita's Rock and in Renouf's Bay, while occasional individuals were found on the frills of *Saccorhiza* from the Rapids.

Patina pellucida (Gastropoda) (Tables 4 and 5 and Figs. 13 and 14), was found feeding on fronds and stipes of *Saccorhiza* throughout the Rapids area. There was considerable variation at any one station in the number of *Patina* per plant. However, in spite of this, it has been possible to establish differences in population density between different stations.

Patina was very scarce on *Saccorhiza* in all places where the current was weak, namely Renouf's Bay (1946, 1947), Eddy Creek (1938, 1946) and near Nita's Rock (1946, 1947). On the other hand, *Patina* was plentiful on *Saccorhiza* in places of moderately strong current, both above and below the Sill (stations B, C, J and K in 1946 and C in 1947 also). This generalization, first reached in 1938, was confirmed in each of the two subsequent visits. Reference to the graph for the 1947 data (Fig. 13, stations M and C) will render superfluous any further statistics concerning this comparison.

Considerably fewer *Patina* were collected in the strong current on the Sill (stations E, F, H) than in moderate current above and below it (stations B, C, J and K). The conclusion that *Patina* was more abundant in moderate than in strong current is fairly obvious from an examination of the data for 1947 (Fig. 13, stations C and E), but statistical treatment is, nevertheless, desirable.

In comparing samples of *Saccorhiza* from different stations it is necessary to take account of the possibility that the number of *Patina* may be correlated with plant size; naturally the plants collected at the various stations were not all alike. In order that the relation between number of *Patina* and plant size might be determined and taken into consideration in comparisons between stations, a very considerable number of plants were collected from only a few stations in 1947. While *Patina* was very scarce at the two stations of low current (stations M and A), the samples from moderate current (station C) and strong current

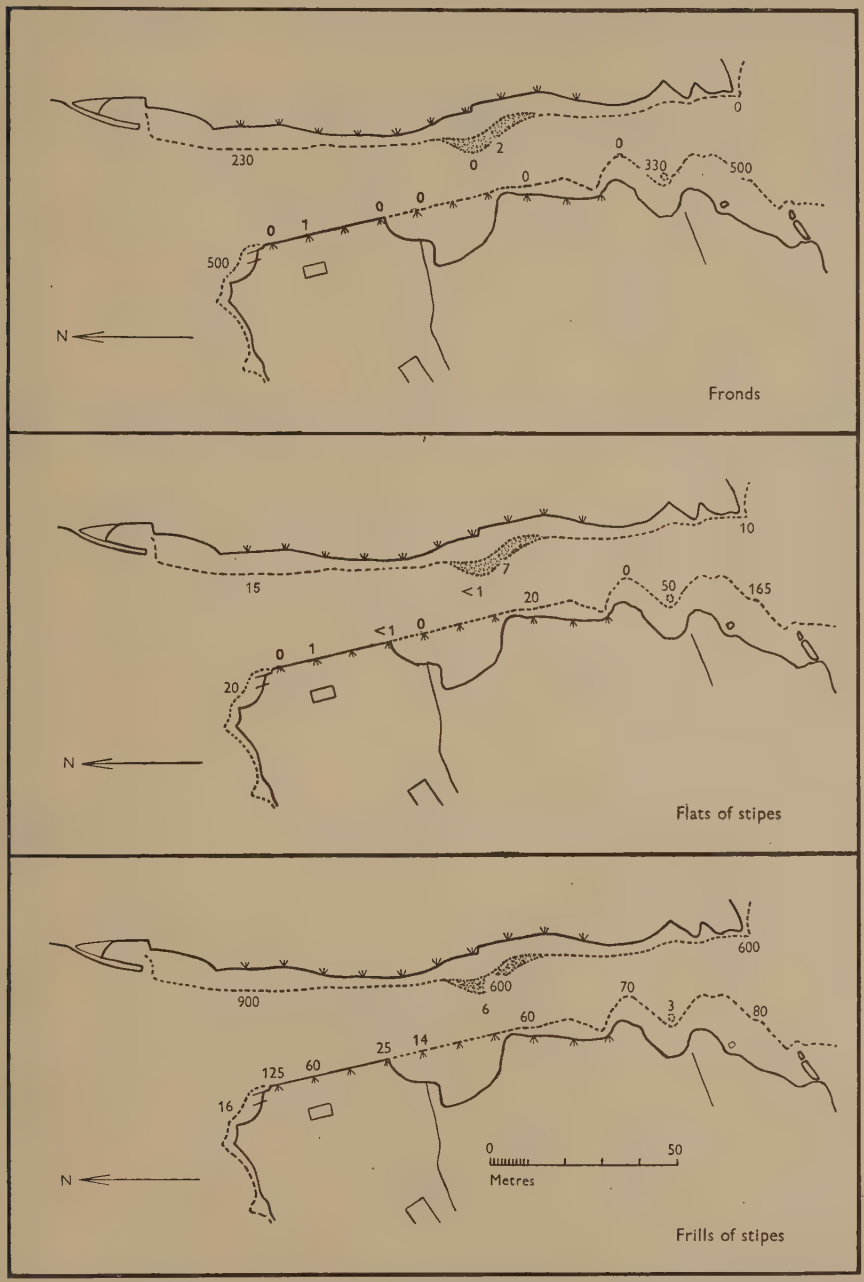


Fig. 7. Average number of colonies of *Hippothoa hyalina* per plant, on fronds, flats of stipes, and frills of *Saccorhiza bulbosa* in September 1946, as determined by counts from samples (Table 2)

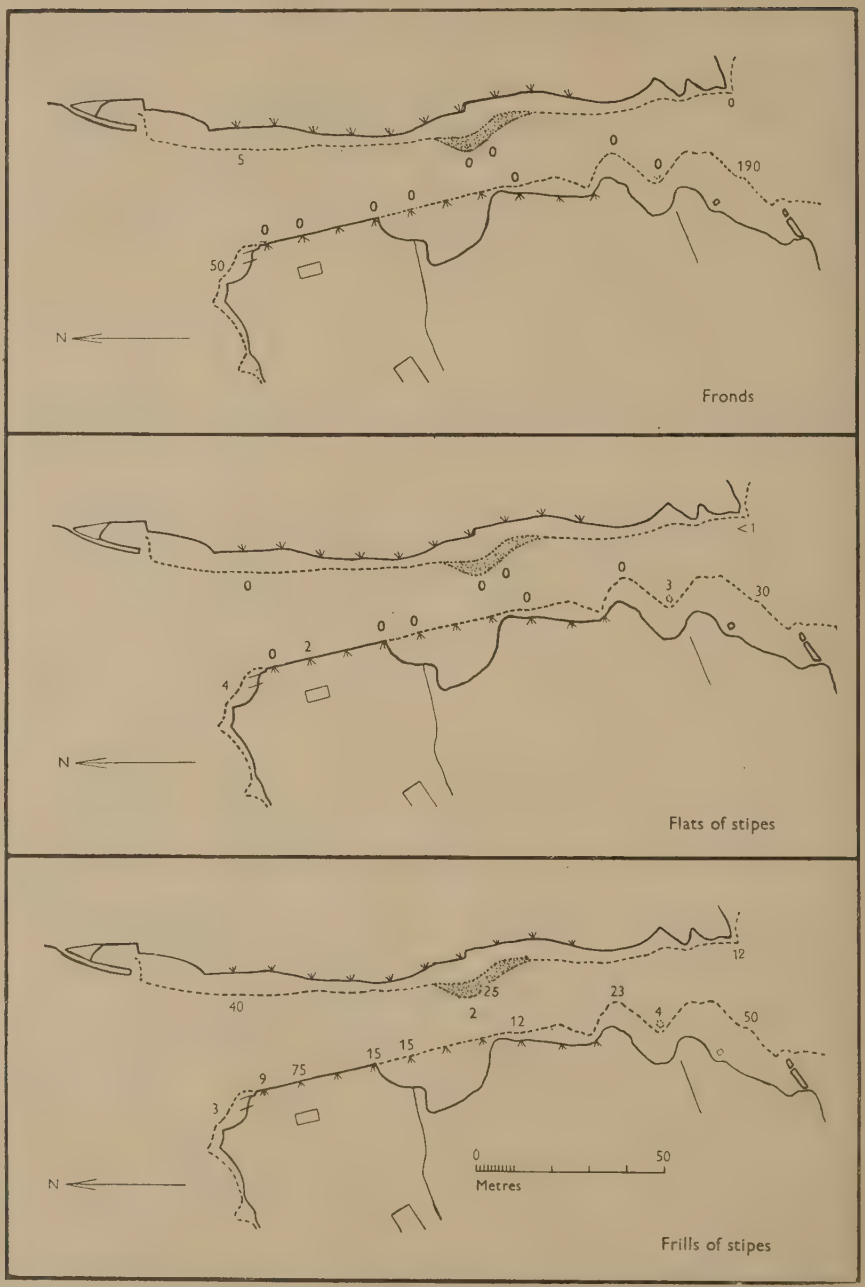


Fig. 8. Average number of colonies of *Tubulipora plumosa* per plant, on fronds, flats of stipes, and frills of *Saccorhiza bulbosa* in September 1946, as determined by counts from samples (Table 2).

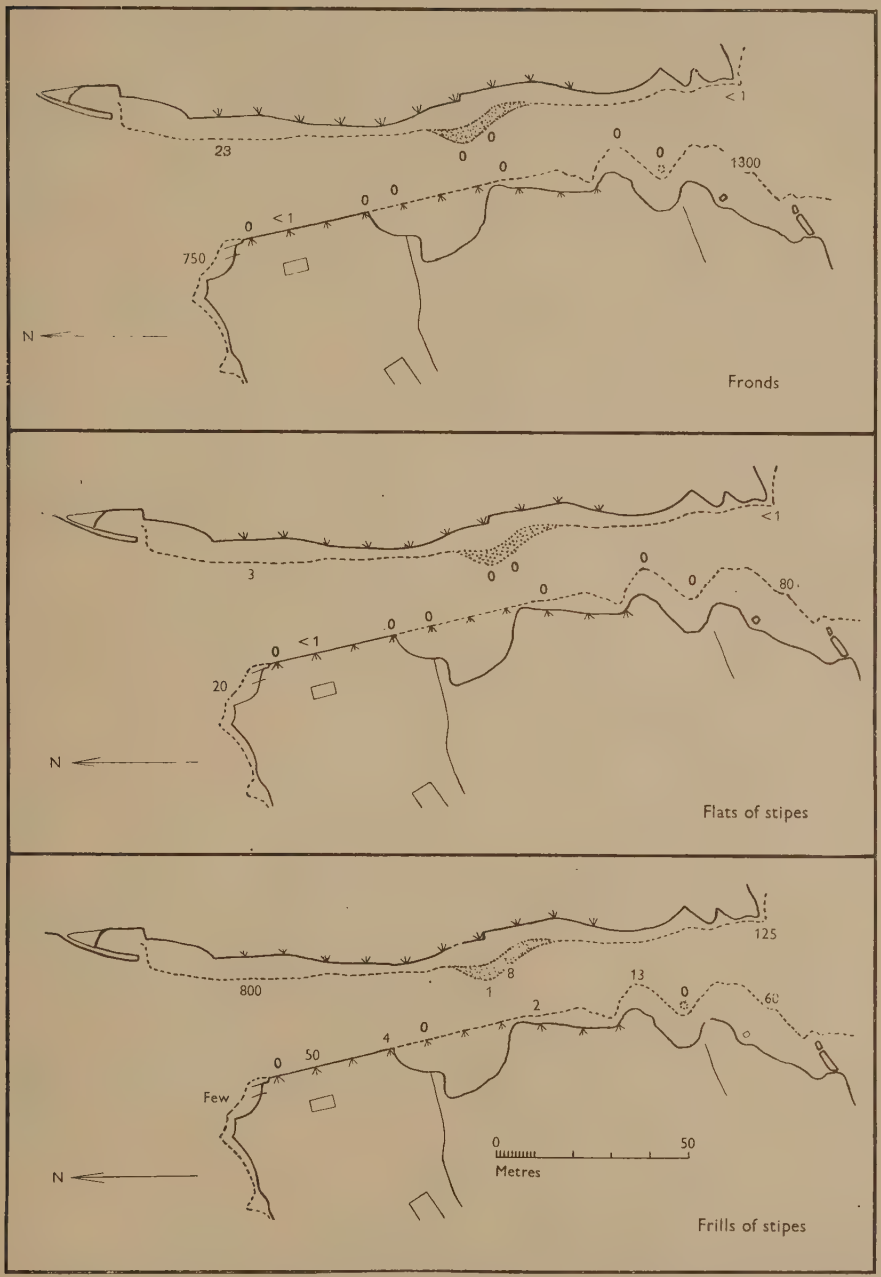


Fig. 9. Average number of anomiid spat per plant on fronds, flats of stipes, and frills of *Saccorhiza bulbosa* as determined by counts or estimates from samples taken in September 1946.

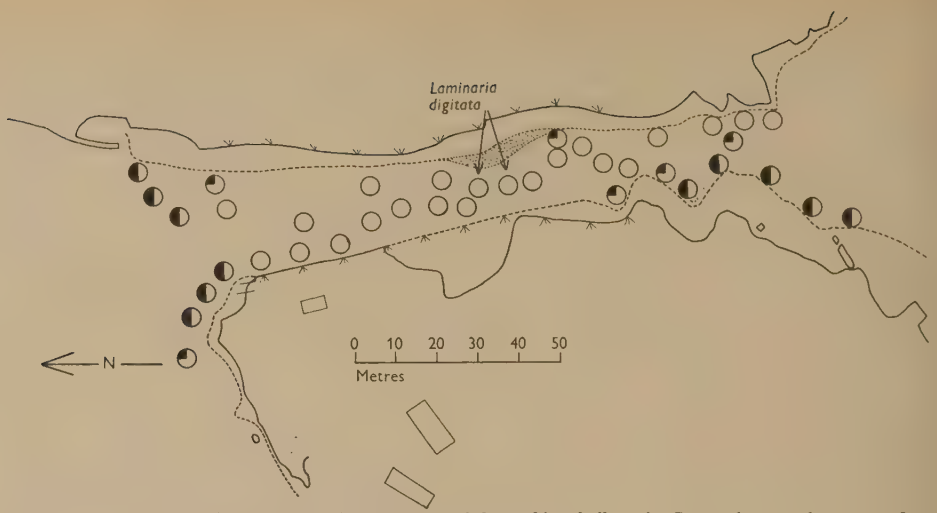


Fig. 10. Distribution of *Gibbula cineraria* on fronds of *Saccorhiza bulbosa* in September 1946 as seen from boat or quay. For explanation of symbols see text (p. 229).

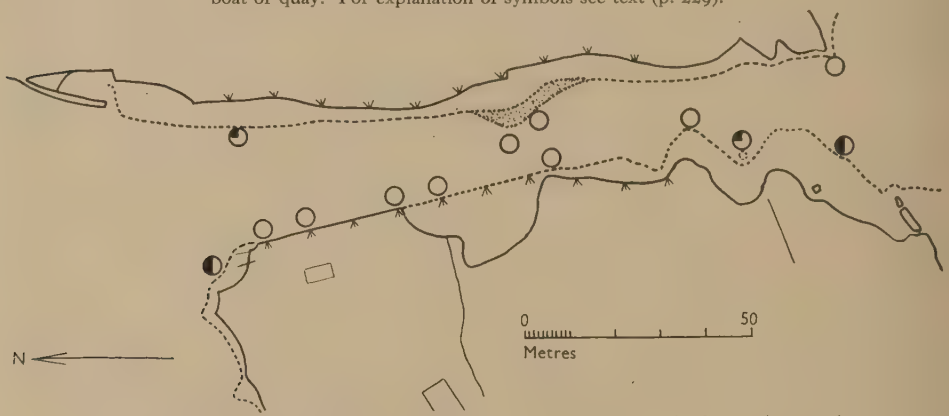


Fig. 11. Distribution of *Bittium reticulatum* on *Saccorhiza bulbosa* in September 1946. For explanation of symbols see text (p. 229).

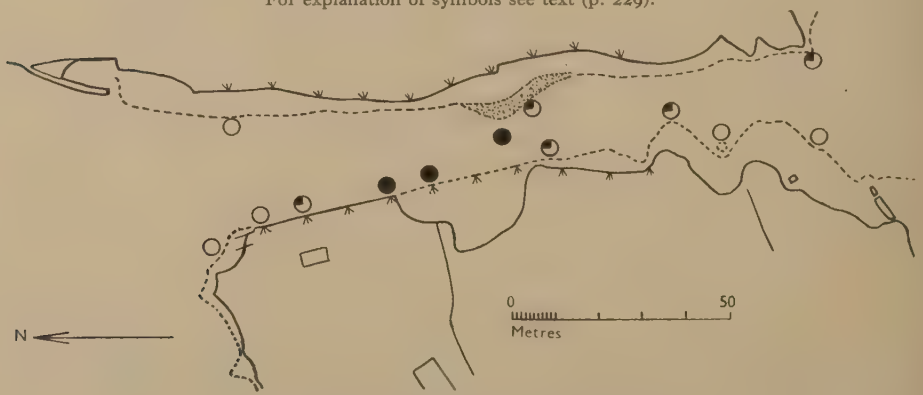


Fig. 12. Distribution of *Jassa falcata* on frills of *Saccorhiza bulbosa* in September 1946. For explanation of symbols see text (p. 229).

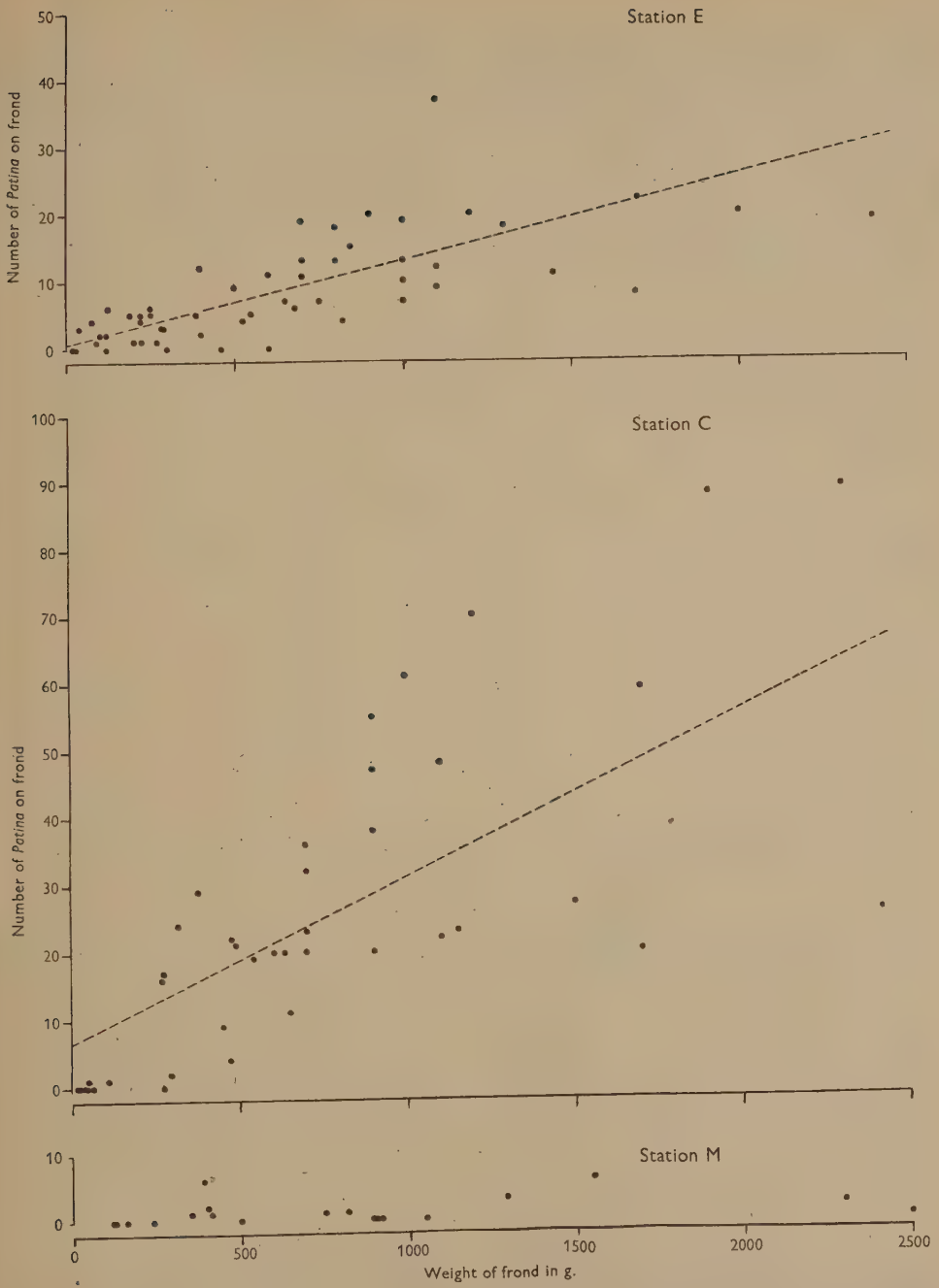


Fig. 13. Numbers of *Patina pellucida* on the fronds of *Saccorhiza bulbosa* at station E (strong current) station C (moderate current), and station M (weak current). July 1947. The broken lines show the calculated rectilinear regressions.

(station E) were sufficient to provide the required information. The numbers of *Patina* found on each frond are plotted against frond weights in Fig. 13, and the calculated rectilinear regressions for stations C and E are also shown. The data for these two stations (C and E) have been compared by analysis of covariance (Mather, 1943), and the difference in *Patina* populations has been found to be highly significant ($t = 5{\cdot}75$ for 90 degrees of freedom). By this treatment due allowance is made for any differences in the weights of fronds collected at the two stations. It should, however, be pointed out that the number of *Patina* might conceivably be correlated with some other variable characteristic of *Saccorhiza*—a characteristic not reflected in the plant or frond weight. For instance, plants of the same weight at different stations might on the average have different surface areas. However, we have no reason, from our studies of the growth forms of *Saccorhiza*, to suppose that this is the case. Although we have not measured the surface areas of *Saccorhiza* from different stations, we have compared a variety of other measurements. Plants from quiet water differ markedly in growth form from those in moderate or strong current, but those in moderate current (station C) and in strong current (station E) have been found to be fairly similar. It therefore seems very unlikely that the considerable difference found in *Patina* populations at these two stations will be explained in terms of growth form of the plant. On the contrary it appears to indicate a real difference in the ability of the animal to establish itself and to survive.

The population of *Patina* at a number of stations scattered throughout the Rapids area was studied in 1946. Only the total weight of each plant and the number of *Patina* on it were recorded. Since only eight plants were collected at each station, and the variability was considerable, it is not possible to determine satisfactorily the relation of the number of *Patina* with plant weight. In order to compensate for the variation in the weights of plants collected at the different stations, it is possible to correct the counts of *Patina* for each plant arbitrarily by dividing by the weight of the plant. This procedure is not strictly justified, but may be used to show that a correction of this sort makes no difference to the conclusions which

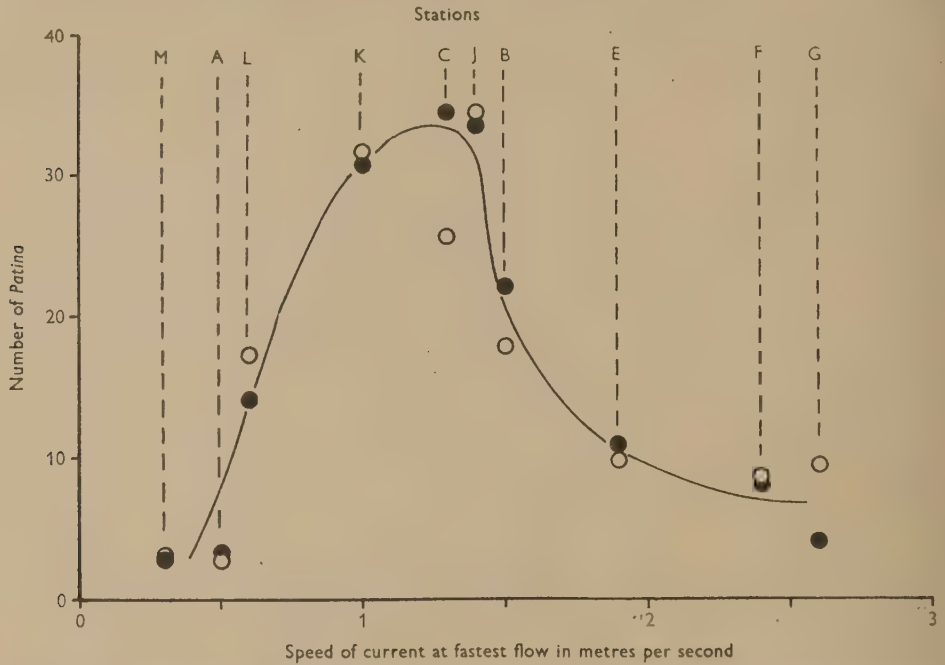


Fig. 14. Population density of *Patina pellucida* on *Saccorhiza bulbosa* (whole plant) in relation to the speed of current at fastest flow (in metres per second). Letters indicate canopy stations. September 1946.

● mean number of *Patina* per *Saccorhiza* plant; ○ number of *Patina* per 3 lb. of *Saccorhiza*.

can be drawn. The results are much the same whether expressed as the number of *Patina* per plant or as the number per unit weight of plant. Both are given in Table 4 and are plotted in Fig. 14. There is a clearly defined maximum at moderate current strength. A similar graph could be obtained from a plot of *Patina* population against total flow, since at the various stations in the Rapids the maximal current and the total flow are closely correlated.

(e) *Experiments on the effects of water current on gastropods*

Since the distribution of various gastropods in the Rapids area is such as to suggest that they are unable to endure strong current, some simple experiments were undertaken for the investigation of this matter.

Table 6. *Tests of the persistence of the gastropod* Gibbula cineraria *on laminarian algae exposed to various degrees of water current*

Test no.	Time stated (G.M.T.)	Duration (hr.)	Alga used	(1) in Rapids: no. of gastropods		(2) in Eddy Creek: no. of gastropods		(3) off Nita's Rock: no. of gastropods	
				Before	After	Before	After	Before	After
1	July 1938	1½	*Laminaria saccharina*	21	1	27	26	.	.
2	1.30 p.m. 9 Sept. 1946	4*	*Saccorhiza bulbosa*	139	2	127	96	72	75†
3	4.00 p.m. 13 Sept. 1946	16*	*Laminaria digitata*	37	0	.	.	25	7
4	6.40 p.m. 17 Sept. 1946	4*	*Saccorhiza bulbosa*	116	20‡	.	.	122	108

* Finished at high slack water.

† A few must have been overlooked in the initial count. In subsequent tests the initial number was determined by subtraction of the number remaining in the tub from the number originally placed in it.

‡ All of these were on a part of the base of the frond which was not properly immersed.

Gibbula cineraria was used since it shows this type of distribution (Fig. 10), is common on the fronds of laminarian algae, and is easily handled.

In these experiments, shortly before low slack water a number of *Gibbula* were allowed to settle on appropriate laminarian algae while in a tub of sea water in a cool place. At low slack water the seaweeds were suspended: (1) in the Rapids at station D (from a pole projecting from the iron ring in the quay); (2) in Eddy Creek in relatively quiet water (from a moored buoy); and/or (3) off Nita's Rock, in quiet water (from a moored buoy).

In one test (No. 3) the experimental seaweeds were held at the sea-bottom and so were liable to touch other seaweeds. In all the other tests they were suspended near the surface, and so were isolated. At the end of the tests the seaweeds were removed for a recount of the *Gibbula* on them.

The results are shown in Table 6. It is clear that almost all the *Gibbula* which were immersed in the Rapids quickly vanished from the seaweed fronds, whilst most of those immersed in Eddy Creek and off Nita's Rock remained.

4. DISCUSSION ON THE EFFECTS OF CURRENT ON THE FAUNA OF THE CANOPY

(a) *Current preferences*

A number of the species studied show a restricted distribution within the Rapids area, with a marked preference for stations of a particular and narrow range of current conditions. In these cases it is difficult to avoid the conclusion that current is the responsible influence, although it may operate through dependent factors. The possibility that differences in tidal or other conditions inherent in the transition from sea to lough are responsible is eliminated by the fact that quiet water stations above the Sill (A, R) and below the Sill (L–N) are remarkably similar in respect of their habitation by these animals, and differ from swift water stations on or near the Sill (E, F and H).

The fauna of the canopy can be classified roughly in terms of distribution with reference to current:

Species most abundant in weak current

Hippothoa hyalina (Polyzoa)
Tubulipora plumosa (Polyzoa)
Scrupocellaria reptans (Polyzoa)
Gibbula cineraria (Gastropoda)
Bittium reticulatum (Gastropoda)
Rissoa parva (Gastropoda) (data somewhat limited)

The species listed above were confined to situations where they were exposed to weak current only.

Species most abundant in moderate current

Membranipora membranacea (Polyzoa)
Patina pellucida (Gastropoda)

Of these two species *Membranipora membranacea* was practically confined to moderate current, while *Patina pellucida* exhibited a wider range, extending in small quantity into weak current and in moderate quantity into the strongest currents on the Sill.

Species most abundant in proximity to strong current (without direct exposure to it)

Jassa falcata (Amphipoda)
Tubularia bellis (Hydrozoa)

Although both these species were most abundant at stations of strong current, they were confined to the frills and bases of the stipes of *Saccorhiza* and therefore were presumably to some extent sheltered.

Other species studied were not obtained in sufficiently large numbers to justify inclusion in the lists given above. In no case have we been able to say that a species was distributed indifferently with respect to current.

It must be pointed out that, while the current preferences of the various animals are correctly summarized above in respect of the Lough Ine Rapids area, this grouping might not apply in other places under different sets of conditions. For instance, if in a particular case an organism showed a preference for a certain degree of current because this was necessary to prevent deposition of silt, in another place where silt was lacking this preference might be changed or even completely lost.

We cannot say, from the data so far available, what features of current action are responsible for establishing the observed preferences. It is possible that maximal current plays a considerable part in restricting distribution, or that the continuous maintenance of a certain level of flow is more important, or—perhaps more probably—that distribution must ultimately be explained in terms of the interaction of these two in a particular combination. A more detailed study of conditions during and near the short period of slack water at the turn of the current might be of interest in connexion with the settling of the larvae (p. 243).

(*b*) *Mechanisms of current action*

Current may influence sublittoral animals in many ways. Moreover, it may be effective at different stages of their life histories. Possible effects of current include:

Dislodgement (of adults or larvae).
Prevention of settlement.
Conveyance of larval stages to sites for settlement.
Supply of planktonic food.
Interference with feeding mechanism.
Suppression of gradients in physical and chemical conditions of the water (temperature, oxygen tension, carbon dioxide tension, acidity).
Removal of sediment, settling diatoms, etc., or other debris.
Restriction of food species.
Restriction of competitive species.

Some of these effects are obviously harmful; others are beneficial; others again are of doubtful quality. The various organisms which inhabit the canopy are likely to be influenced by them in different ways and in different degrees. In some cases it is to be expected that beneficial and harmful effects will act in opposition, so that there may be a range of conditions of current within which survival of the species is possible. At lower currents the beneficial effects would be inadequately felt; at higher currents the harmful effects would be too great. Such a balance might account for the maxima shown by *Membranipora membranacea* and by *Patina pellucida*. Fischer (1929), from observations on the shores of 'la Rance', has inferred that certain species, including the sponge *Halichondria panicea*, are favoured by moderate rather than by weak or strong current. However, as far as concerns the Rapids area, for the majority of species the maximal population density is found in the weakest current; it seems probable that the adverse effects of current action predominate in determining their distribution. This does not imply that slight current may not be beneficial or even requisite to these species, since our survey does not include any areas of negligible water movement.

The various effects of current listed above are typical of water movement in general, whether this takes the form of currents which set in a definite direction for a substantial period of time, or whether it results from wave action and therefore undergoes rapid fluctuations in direction and intensity; although naturally the relative importance of these various secondary effects is likely to be different in the two cases. We hope to compare the effects of wave action and of current in the Lough Ine area more extensively on a future occasion.

We are not yet in a position to analyse the effects of current on the various organisms concerned. Of the various possibilities, dislodgement was the most obvious one to investigate first. Our experiments on *Gibbula cineraria* (p. 241) show that it can be effective, although it is not necessarily the only factor operating against this organism. It seems likely that mechanical action of this sort may be a serious problem for many

sedentary or encrusting organisms at the time when their larvae must settle and adhere. This question might be determined by observations of settlement of larvae, as has been done in the case of barnacles (Smith, 1946*a*, *b*). Also it may be possible to move such organisms in the adult stage to places where the current is strong and to determine whether they are able to live and grow provided that they are already well established. Experiments of this sort are now being prepared.

The distribution of plankton in the Rapids area will be dependent on current. The number of larvae ready for settlement which pass different stations will clearly depend, among other things, on the total water flow at those stations. Whether in practice this factor materially influences the density of distribution of various organisms is unknown. Most of the animals studied show a preference for the quietest water, so that in these cases it must be presumed that other overriding factors determine the final distribution.

However the distribution of plankton by the current may be important in another way, since plankton forms the food of so many sedentary animals. Moore (1935) has stressed the importance of water movements, whether due to wave action or to current, in supplying food to the barnacle *Balanus balanoides*. From the estimates of total flow (Table 1) at different stations in the Rapids, one can realize the enormous differences in the rates at which individual items of planktonic food will be delivered to plankton-eating animals at the different stations. How these differences will affect the feeding process cannot be stated, since the nature and density of the plankton in the Rapids has not been exhaustively investigated and since nothing is known as to the relation between feeding and the numerous factors involved.

Many physical and chemical conditions of the water are influenced by current, which tends to destroy local gradients. These conditions include temperature, salinity, oxygen tension, carbon dioxide tension and acidity. The figures for water temperature given in the first paper of this series (Bassindale *et al.* 1948) show that in such relatively stagnant places as Eddy Creek there may be marked deviations from the temperature of the general body of water passing through the Rapids. And where this is true of temperature, so it is likely to be of other water conditions.

The deposition of silt is dependent on changes in current. Also films of small particles, diatoms, and so forth over the fronds of seaweeds and the surfaces of boulders may be established in quiet water. Such deposits may perhaps be unfavourable to certain encrusting Polyzoa. Certain animal species may compete successfully with and so exclude other animals from conditions of current otherwise favourable to both, or one species dependent on another for its food may be restricted by the limited distribution of the latter. The possible ramifications of the influence of current in the ecological structure of a sublittoral community are so extensive and complicated that it would be useless to attempt to discuss individual cases until carefully planned experiments have been carried out.

5. SUMMARY

1. The bed of the Lough Ine Rapids is covered by large laminarian seaweeds, mainly *Saccorhiza bulbosa*. The fronds form a dense canopy, which has a typical fauna associated with it.

2. A study has been made of the speed of the water current at the level of the canopy throughout the tidal cycle (12½ hr.) at a series of selected stations. The total lengths of water-columns passing and the maximal speed of the current at each station are given in Table 1. The various stations range, in maximal speed of current, from a very low value up to 2½ m./sec.

3. An investigation has been made of the distribution of animals associated with the canopy. This investigation comprises both general observations made throughout the Rapids area and a detailed study of samples of *Saccorhiza* collected at the stations mentioned above. Of the animals studied six species (three polyzoans and three gastropods) were confined to situations where they were exposed to weak currents only, that is, on the fronds of *Saccorhiza* at stations of quiet water and in some cases in the shelter of the crenulated margins ('frills') of the stipes at stations of stronger current. Two species (the polyzoan *Membranipora membranacea* and the limpet *Patina pellucida*) favoured moderate current and were less abundant in weak or strong current. Two species (the amphipod *Jassa falcata* and the hydroid *Tubularia bellis*) favoured proximity to strong current but not direct exposure to it.

4. In experiments with the gastropod *Gibbula cineraria* it was shown that the adult animal was washed off *Saccorhiza* by strong currents.

5. There are many ways in which current may directly or indirectly influence the distribution of animals in an area such as the Lough Ine Rapids. Moreover, it may act differently at different stages of the life histories of these animals. Although current is no doubt of paramount importance in the Lough Ine Rapids, the interpretation of the complex interaction of its many effects upon the animals must await much more experimental evidence and must be approached with great caution.

6. ACKNOWLEDGEMENTS

This work has been organized from the Department of Zoology of the University of Bristol. We are glad to acknowledge the critical interest and strong support of Prof. J. E. Harris. At Lough Ine we received every

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We are indebted to Dr E. F. Gibbs (University of Bristol) for the loan of a Watts current meter and for advice on its use; to Mr H. Todd (University of Bristol) for advice on statistical matters; to Dr A. B. Hastings (British Museum of Natural History) for determining samples of the Polyzoa; and to Mrs E. W. Sexton for valuable help with the amphipod genus *Jassa*.

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STUDIES OF THE BEHAVIOUR OF THE TSETSE-FLY, *GLOSSINA PALLIDIPES*, IN THE FIELD: INFLUENCE OF CLIMATIC FACTORS ON ACTIVITY

By F. L. VANDERPLANK
*West African Institute for Trypanosomiasis Research, Nigeria**

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1. INTRODUCTION

The economic importance of the tsetse-fly (*Glossina*) is well known. Man and domestic animals are prevented from utilizing vast areas in tropical Africa owing to the presence of one or more species, most of which are known to be vectors of human or animal trypanosomiasis or both. To combat this menace it is important to obtain a complete knowledge oft he distribution of the various species. It would also be of great value if at the same time some indication of the true density or population of each species could be obtained. Sampling can be carried out by means of various attractant baits or 'trapping' screens, and a standardized method can be obtained to suit each particular type of species and country. However, even with standardized methods of sampling the catch varies daily and from day to day in the same area. This variation in catch is due to variations in the activity of the fly. Activity varies with sex, age and hunger state. Males are comparatively inactive during the first 4–6 days after emergence from the pupal stage, owing no doubt to their sexual impotence. After this initial period they are relatively active for the rest of their lives, and when not seeking food, are actively seeking females. On the other hand, females are comparatively active for the first week after emerging, but once mated and inseminated, become relatively inactive, only becoming active when hungry. They mate during the first 6–7 days after emerging from the pupal stage. Generally very few females are encountered in the field, but the numbers depend on the methods of sampling. Normally only males are utilized for population and activity estimates. Neither age nor hunger cycle of the fly should, or does, cause any rapid fluctuations in density, since the birth-rate in a slow-breeding insect like *Glossina* only varies steadily from season to season, and the hunger cycle is spread over several days and individuals in all stages will be encountered. The variations in the hunger cycles have been studied by Vanderplank (1947), and others. The mean hunger state of a population can be estimated and correlated with activity, but its effect will be masked by the rapid daily variations in activity.

It was considered that if the various factors that affect activity in the field could be separated and their effects measured, it would be possible to estimate the true density (or population) from the results of a standardized catch with concurrent measurements of these factors. To ascertain this, standardized catches were carried out together with periodic measurements of all probable factors. The data obtained were then analysed by statistical methods.

The relative attractiveness of various baits and methods to catch *Glossina pallidipes* (Austen) has already been described by Vanderplank (1944), also

* This investigation was carried out while Research Entomologist to the East African Tsetse Research Organization, Tanganyika.

the effects of the lunar cycle upon activity (Vanderplank, 1941). The methods used in these observations consisted of catching flies that settled on a stationary ox, both inside and outside the fly's home environment. For a detailed description of method and locality, see Vanderplank (1944). It has been found that temperature, humidity and light intensity (or radiated heat) have a marked and immediate effect upon activity of *G. pallidipes*, also that the hunger state and lunar cycle have a slower (spread over several days) effect (Vanderplank, 1947), but that wind velocity and barometric pressure as encountered in the experiments did not show any detectable effect upon activity.

PART 1. THE EFFECTS OF TEMPERATURE AND HUMIDITY UPON THE ACTIVITY OF *GLOSSINA PALLIDIPES*

2. Methods

Before a problem of this nature is tackled there are numerous considerations to be taken into account. In the first instance, what information can be gained from standardized catches? This can be answered by the generalization (Williams, 1940) that

$$\text{Catch} \propto \text{Activity} \times \text{Population}.$$

The activity is affected by a number of different factors, as stated above.

The method of catching will also affect the numbers taken, for a moving catch takes a greater number of tsetses than a stationary catch per unit of time, and so on.

The data used in working the correlations were collected from stationary catches on an ox during the period from June to October 1940. The catch was recorded as the numbers of males or of females caught per quarter-hour throughout the day, together with the air temperature, wet and dry bulb (whirling hygrometer), light intensity, black-bulb temperature, wind velocity and barometric pressure.

Whereas fly catches are commonly regarded as furnishing a measure of the density-activity of the tsetse, the author regards those which follow as indicative of fluctuations in activity almost entirely, for identical conditions of temperature and saturation deficiency give roughly equal catches in different months. Thus the total flies caught during July in 26 quarter-hours, when the dry- and wet-bulb temperatures varied between 27 and 32° C. and 17 and 23° C. respectively was 53 tsetses, as compared with 54 during October from another 26 quarter-hours with wet- and dry-bulb readings respectively identical with the above (detailed figures in Appendix 1).

Further, recaptures from marked flies have provided estimates of population which show little change during the period June to October, which was specially chosen on this account.

The author therefore proposes, in the arguments which follow, to regard the variation of fly catches as measures of variation in fly activity.

Jack & Williams (1937) have shown with *G. morsitans* that at temperatures from 30 to 32° C. and above they avoid light and seek shade. These experiments have been repeated by the writer in the laboratory with male and female *G. pallidipes* and with the result that they react in a similar manner but at slightly higher temperatures, from 32 to 34° C. But it appeared that the intensity of the light and humidity also affects this reaction and the critical temperature. Dry conditions raise the critical temperature whereas high humidities lower it. This may be connected with the internal thoracic temperature of the fly, since the fly appears to be able to increase or lower its internal temperature under certain conditions for a limited period, and the usual internal temperature when active is about 30–32° C. (Vanderplank, unpublished).

It has been found by examination of the data that there are approximately the same number of observations for each unit of temperature, and they cover the complete range of light intensities recorded. For example, at a temperature of 30° C. approximately, equal numbers of catches have been made at low, medium and high light intensities; the result will be to eradicate the effects caused by light, although the fly's decreased activity after 30° C. may be due to the temperature effect on its reaction towards light. The same applies to the lunar cycle, the effects of which have been described by Vanderplank (1941).

Since the amount of moisture carried by the atmosphere is largely dependent on the temperature, it is not easy to separate its effects upon activity of the tsetse. However, sufficient data have been obtained to analyse these by considering the effects of humidity at different temperature levels.

Williams (1937, 1940) has already pointed out that catches of insects under varying climatic conditions do not show normal distribution curves and that a normal distribution can often be brought about by converting the catch-plus-one into logarithms and using the numbers obtained in the same way as actual numbers. This has been done with the following observations. As Williams (1940) points out, there is sometimes a large number of zero catches which produce an appearance of skewness even in the logarithmic curves (e.g. temperature group 32° C.), because it is not possible to catch a portion of a tsetse, and so the zero catches include those which one would expect to catch between 0 and 1 insects.

3. Activity in relation to temperature and humidity

The old male catch on oxen during the period from June to October 1940 was analysed in the following manner. The observations were divided into 'temperature groups' so that all the quarter-hour catches carried out at 30° C. fell into one group, and so on for each temperature. The catches of old males in each of these temperature groups were then correlated with their corresponding saturation deficiencies, giving the activity of the fly in relation to humidity at constant temperature. These data are summarized in the form of correlation tables in Appendix 2 which show the actual values of each correlation.

Table 1

Temperature groups (° C.)	No. of observations	Correlation coefficients of log catch-plus-one with sat. def.	Regression, proportionate change in catch for a rise of 2 mb.
19–25	58	+0·6624	×1·082
26 and 27	98	+0·5128	×1·138
28	225	+0·3161	×1·056
29	400	+0·2310	×1·035
30	369	−0·0455	×1·9955
31	304	−0·4285	×1·9551
32	342	−0·3223	×1·9791
33	114	−0·6716	×1·9177
34	56	−0·6955	×1·8719
35	40	−0·9018	×1·8152
Total observations	2006		

It will be seen from Table 1 that the strength of the correlation of activity with saturation deficiency decreases from 19 up to 30° C., when it is no longer significant, then as the temperature rises further the correlation increases again, but the relation between activity and saturation deficit is reversed. All these correlations are significant, *P* being less than 1 in 100, except in the 30° C. temperature group. Temperature group 32° C. does not fall exactly in line with the others and the reason for this is obscure. Like the correlations the regressions of catch on saturation deficit decrease with two slight discrepancies up to the temperature group 30° C. where practically no regression exists, then they increase in value but are reversed, the catch falling instead of rising with the increasing dryness of the air. It should also be noted that each temperature group correlation is significantly different from its neighbours except groups 29 and 30° C., 30 and 31° C., the two groups on either side of the critical temperature group 30° C.

4. Discussion

In earlier work on this subject by the author (unpublished) and by Moggridge (1940) no attempt was made to separate the data into temperature groups. Consequently the results of correlating *G. pallidipes* activity with saturation deficiency at Shinyanga always showed a positive correlation. However, Moggridge at Kilifi in Kenya found a negative correlation, except early in the day under very hot and dry conditions. It was thought that the reversal at 30° C. of the effect of saturation deficiency might explain the contradictions, but it appears from further examination of Moggridge's unpublished data that the negative correlation under Kilifi conditions continues to operate well below the critical temperature of 30° C. The discrepancy thus remains unexplained.

The activity of male *G. pallidipes* has also been correlated with temperature at different humidity levels, and the change over from a positive correlation to a negative one occurs at a saturation deficiency of 25 mb. The activity of female and of total (male and female) *G. pallidipes* has been correlated with saturation deficiency at different temperature levels and vice versa, with very similar results to those given for the male flies. The data have not been given because they are so similar to those of the male alone. Observations have been made at different seasons and years and treated in the same way giving similar results. Data obtained from catching flies on various baits other than ox (screen, man, sheep and pig) on both moving and stationary catches have been treated with similar results.

PART 2. THE EFFECTS OF RADIATION UPON ACTIVITY

5. Preliminary observations

It was noticed that *G. pallidipes* were caught in greater numbers during the early morning and late afternoon outside their home environment (thickets), whereas in the thickets there was merely a slight decrease at midday. This has been recorded by other workers (Croveri, 1919; Curson, 1924; Mossop,

1928; Fuller & Mossop, 1929; Harris, 1930; Swynnerton, 1936; Henkel, 1937; Jack, 1941).

Plotting the mean catch of either male or female flies against the time of day revealed that the large numbers taken during the early morning decreased until midday (sun-time) and then increased until sunset to such an extent that the evening catches were higher than those of the morning; this gave an irregular U-shaped curve. After corrections for the effects of air temperature and humidity, the resultant curve was a regular U-shaped one. Both these curves gave highly significant correlations with either light intensity or solar heat radiations.

It was impossible in the field at the time of the experiments to separate completely 'visible' light from radiated heat. So the term *light intensity* in this paper refers to measurements of approximately 75 % visible light between 4000 and 8000 Å. units, some 23 % heat radiations and approximately 2 % ultra-violet. Similarly, radiated heat refers to measurements made by a black-bulb thermometer *in vacuo*, and this measured approximately 60 % infra-red and 40 % of the visible light. No doubt with suitable apparatus various monochromatic bands of visible light, ultra-violet and infra-red radiations could be accurately measured and correlated with the activity of the fly. However, so far there is no evidence that the fly is affected by any particular band of light, but data do suggest that activity is reduced by a combination of intense light and heat radiations. The purpose of these investigations was to find whether light intensity (with other radiations) affected activity, and if so, whether activity could be correlated with some relatively simple method of measuring these radiations in the field. If the results were to be of any practical use the measuring apparatus must be portable, so that the catch could be corrected for a predetermined constant. Either of the two methods described here are suitable for this purpose, but both are too closely connected with each other to separate their effects on the activity of the fly.

6. Methods

A photoelectric cell of a selenium rectifier type, which was later compared and graduated in foot-candles against a standard instrument was used to measure light intensities. Since these observations were spread over a considerable period (only a portion of the observations are used in this paper) it was necessary to devise some method to ensure that the light intensity from the same area was measured on each occasion. Light intensity varies with:

(*a*) the angle of the sun as determined by latitude, season and time of day;

(*b*) altitude;

(*c*) weather, degree of cloudiness, amount of water vapour and dust in the air;

(*d*) colour of vegetation (green vegetation will absorb more light than bleached dry grass).

The photoelectric cell was used in conjunction with a reflex camera. A square of 50 × 50 ft. was marked out in both sites where the catches were made, and a position for the camera was marked 60 ft. to the north of the square. The camera was set 4 ft. above the ground level; it was directed and focused so that the marked area appeared on the ground-glass screen, the rest of the picture being obscured by an opaque mask. The photoelectric cell was fitted over the exposed area of the screen with an ultra-violet absorbing filter inserted between it and the screen. The light intensity of the constant catching area was then measured in unit divisions of the galvanometer deflexion during each series of observations. Later the photoelectric cell was graduated against a standard instrument and the approximate readings in foot-candles are given with the unit deflexions.

Comparative readings were carried out in the field using (*a*) the camera set-up, (*b*) the photoelectric cell without the camera and pointing towards the experimental area, and (*c*) pointing to the open sky in the north, away from the sun. The readings were taken at quarter-hour intervals throughout one day. Position (*c*) gave, as expected, the greatest maxima and variation in intensities, and (*a*) the least; (*b*) being intermediate between the two and about one-quarter the intensity. All three readings vary in the same proportions and so all would equally well correlate with the fly's activity. This will be considered again later in the paper.

The solar heat radiations were measured by a black-bulb thermometer in a vacuum; it is not possible to standardize these instruments but a single thermometer gives intercomparable readings.

7. Daily and monthly variation in light intensity and radiated heat

The temperature registered by the black bulb varied in proportion to the light intensity, except that the former remained higher during the afternoon because of radiation from the hot ground, rocks, dead trees, etc. A typical comparison between the black-bulb temperature and light intensity on a cloudless day is shown by the hourly means in Table 2, which is founded on a single day.

These figures are the actual figures from observations taken concurrently with catches of *G. pallidipes* and *G. swynnertoni* on an ox tethered to a *Commiphora* tree in a small hardpan area on 17 April 1941.

The monthly variations of both light intensity and black-bulb temperature readings depend on the declination of the sun, the degree of cloudiness and the amount of dust in the atmosphere.

The colour of the vegetation would also affect the amount of light reflected; however, the following

comparative figures were obtained by exposing the photocell to the sky at noon, but away from the direct sunlight and clouds, and show the monthly variations of both light intensity and black-bulb thermometer readings. Readings were taken only on cloudless days (i.e. less than one-tenth of the sky covered with clouds). It will be seen that the black-bulb temperature is correlated closely with the light intensity, not only in its daily but also in its monthly variation.

honey-bee was influenced by ultra-violet intensity but their data showed an association between variations in honey-bee activity and the radiation of clear light.)

The 'home' environment used in these experiments was a thicket of *Euphorbia tirucalli* L. which has already been described by Vanderplank (1944). The maximal light intensity (foot-candles) was only one-sixth of that of open country.

Table 2. *Comparative hourly means of light intensity and black-bulb thermometer in vacuum, taken in a hardpan area, 17 April 1941*

Sun-time ...	7	8	9	10	11	12	1	2	3	4	5	6
Light intensity units	3	9	21	30	37	45	39	25	20	13	8	1
Approximate foot-candles	1·2	13	50	100	170	300	190	75	50	30	11	1
Black-bulb temp. (° C.)	20	24½	32	43	47	52	52	51½	41	33	32	27

(The light intensity and the black-bulb thermometer readings were taken simultaneously in hardpan (*Commiphora-Lannea* and short-grass) areas. Readings would be higher in open country.)

Table 3. *Monthly maximal light and black-bulb temperature readings at noon*

Month ...	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Light intensity	49	51	54	48	41	39	37	43	45	50	48	46
Approximate foot-candles	380	430	575	360	225	190	162	260	300	400	360	325
Black-bulb temp. (° C.)	70·6	70·0	75·5	66·5	63·7	61·8	60·8	64·0	64·3	71·2	68·0	65·2

Old Shinyanga is situated in latitude 3° 33′ S., and the sun is directly overhead during the first weeks of March and October, when both the light intensity and the black-bulb temperature reach their maxima. However, neither light intensity nor radiated heat is as high during October as at the March equinox. October comes at the end of the dry season; and after the 4 or 5 months of drought, high winds and bush fires there is a vast quantity of dust in the atmosphere which reduces the intensity of the solar radiations, and there is as much as 31·5 % difference between the maximum light intensities for March (equinox) and for July (early dry season when the sun is north of the equator). This is a very large difference, especially when we remember that the vegetation is green during March and absorbs more light than the dried grass and leafless trees of July.

8. Activity in the 'home' environment

As stated above, a stationary ox was used as bait for *Glossina pallidipes* in these experiments. Any differences in the numbers caught between the quarter-hour periods must be due to a variation in activity. This would not be true of moving catches, because the density of the tsetses changes with the vegetation; this is particularly noticeable with *G. pallidipes*. With stationary catches, however, the fly has to be sufficiently active to seek out and go to the bait animal. (Butler & Finney (1942) took the numbers of bees observed to leave the hive every 7½ min. as an index of activity. Previous work had suggested that the

During the preliminary observations carried out from January to October 1939, neither light intensity nor black-bulb temperatures were taken, the catch merely being recorded against time of day. The results of this series are given below in Table 4.

Table 4. Glossina pallidipes *catch against time of day. 'Home' environment in* Euphorbia tirucalli *thickets*

Hour-period (sun-time)	No. of ¼ hr. catches	Average *G. pallidipes* per 7½ hr. catching: Males	Females	Total
9.00–	57	33·4	19·5	52·9
10.00–	97	34·0	19·8	53·8
11.00–	97	22·9	22·3	45·2
12.00–	97	20·7	24·7	45·4
1.00–	97	15·2	29·4	44·6
2.00–	97	13·9	37·4	51·3
3.00–	97	11·5	33·1	44·6
4.00–	97	24·4	56·6	81·0
5.00–	24	30·0	37·5	67·5

It will be noticed in Table 4 that the female catch increases throughout the day, reaching a peak between 4.0 and 5.0 p.m., whereas the male catch decreases up till 3.0 p.m. and then increases. The total (male and female) catch follows an irregular U-shaped curve. Activity is, however, influenced by humidity and temperature, and when the catch is corrected for a constant humidity and temperature a regular U-shaped curve results. The mean catch for each period was corrected from the regressions obtained from correlating temperature and humidity

with activity. The data in these observations were equally spread over all light intensities, and the methods used for correcting the catch were similar to those described by Williams (1940). These data have been described separately by me in Part I.

The correlation between the corrected mean *Glossina pallidipes* catch (data from Table 4) and the *observed mean* light intensity (expressed as galvanometer units, the readings being taken in the same site as the catches but on a different occasion) was significant with r equalling $-0{\cdot}97$ when n' equals 757, giving P less than 0·01.

In other observations, carried out in the same locality in October 1940, the mean light intensity and the black-bulb temperature were recorded for each quarter-hour against the male and female catch for the same period. The logarithm of the total (male and female) catch-plus-one was then correlated with the light intensity and with the black-bulb temperature: the former gave a figure of $r=0{\cdot}53$ when the number of observations was 200; the regression of fly on light intensity showed that when the light intensity was 24 units (approximately 52 f.c.) the catch was 2·6 flies per quarter-hour: but when the light intensity was 4 units (approximately 0·4 f.c.) then the catch was 5·8 flies per quarter-hour. The correlation of the *G. pallidipes* catch with the black-bulb temperature gave $r=0{\cdot}43$ when n was 200, and the regression of fly on temperature showed that when the temperature was 47° C., the catch was 2·3 flies per quarter-hour; and when the temperature was 29° C., the catch was 5·4 flies per quarter-hour. Both these correlations were highly significant. Further, since the correlation of *G. pallidipes* catch with light intensity is significantly the higher of the two, it would be the more accurate method to use in the field for subsequent correlation of numbers caught.

The question arises in this type of observation whether the catch, with or without negative results, should be correlated with light intensity measurements, or whether some attempt should be made to correct for the skewness of the distribution of the catch, which is caused for the most part by the presence of negative results. Fisher states (in a letter to Dr Jackson) that normal distribution is not essential for correlation. In each case, the catch with and without negative results, the catch-plus-one, also the logarithm of the catch-plus-one have all been correlated with the light intensity or other data. It was found that similar results were obtained by each of these methods, and were not significantly different from each other. The regressions also fall within more or less the same limits.

9. Activity outside the 'home' environment

Similar experiments were carried out in a hardpan area bordering riverine thickets inhabited by *G. pallidipes*. The catching station was situated about a hundred yards away from the fringes of the riverine thicket in short grass with a few evenly spaced *Commiphora* and *Lannea* trees.

All-day catches on a tethered ox were carried out monthly from October 1940 to July 1941. The male and female *Glossina pallidipes* and *G. swynnertoni*, as well as other blood-sucking insects such as *Tabanus*, *Pangonius* and *Haematopota* were recorded for each quarter-hour, together with the current mean air temperature, relative humidity, evaporation rate, saturation deficit, wind velocity, barometric pressure, black-bulb temperature and light intensity.

Once again, when either the total *Glossina pallidipes* catch or the male or female catch separately, for each of the monthly groups, is correlated with either light intensity or black-bulb temperature, a significant result is obtained, and the correlation with light intensity is significantly higher than with black-bulb temperature. The regressions of fly on light intensity or fly on black-bulb temperature vary slightly with the density and hunger cycle of the fly during any one month, but both show that exceptionally few flies are taken when the light intensity is above 35 units and the black-bulb temperature is above 61° C. The time of day and the seasons when these limits are exceeded can be gauged from Tables 1 and 2. These figures can be taken as the upper limits for full activity for a cross-section of the *G. pallidipes* population in normal conditions. Since the maximal light intensity in July (early dry season) is only 37 units, it will be seen that *G. pallidipes* can then be active almost throughout the day, although the maximal activity is still in the morning and evening. The results of correlating the total *G. pallidipes* catch with light intensity and black-bulb temperature in December 1940, a cloudy month during the short rains, and in June 1941, a nearly cloudless month during the early dry season are given in Table 5.

Table 5.

Correlation of total (male and female) *Glossina pallidipes* catch with light intensity:

December 1940	$r=-0{\cdot}72$	$n=200$
June 1941	$r=-0{\cdot}82$	$n=212$

Correlation of total (male and female) *G. pallidipes* catch, same data as above, with black-bulb temperatures:

December 1940	$r=-0{\cdot}52$	$n=200$
June 1941	$r=-0{\cdot}62$	$n=234$

Note: P is less than 0·01 in each of these correlations.

These suggest that *G. pallidipes* activity is continued after dark. The flies have been caught in the evenings in large numbers until darkness has stopped further work, and a few have been taken at night (Vanderplank, 1941). Laboratory observations

suggest that activity continues at night as long as the temperature does not fall below 18° C., and the night is not absolutely 'black'.

To test whether *G. pallidipes* was active at night, some 10–30 individuals were liberated at night on different occasions in a room about 8 × 8 × 3 m. Light from the stars, or stars and moon, was admitted through two gauzed windows on either side; each window was approximately 2 × 2 m. On other occasions the room was completely blacked out. When some star or moonlight was available I was bitten by numerous flies and, as far as possible, I killed each fly as it bit. Some 25–50 % of the numbers liberated were killed during the course of the evening. When the room was 'blacked out' only an occasional fly bit. Other experiments have shown that *G. pallidipes*, also other species of *Glossina*, are attracted to ultra-violet light below 3000 A., and that they are also attracted to a black-body heat source of 200° C. in the absolute dark.

These experiments show that a wide range of light and radiated heat can attract *G. pallidipes*, and that it is not influenced by any particular wave-length group. Since previous authors have been concerned with the activity of *G. pallidipes* at different times of the day, it will be of interest to include a table of male and female *pallidipes* catch against time, taken from this hardpan catching area, and directly comparable with Table 4 of this paper. This group of observations was carried out on sunny days during June 1941.

G. pallidipes were caught throughout the day, but those tsetses that were taken between the hours of 11 a.m. and 2 p.m. were caught during 3 days only out of the total 11 consecutive days (17–27 June inclusive) on which the observations were carried out, when the light intensity owing to a smoke haze did not exceed 33 units (approximately 125 f.c.). Since the maximum light intensity recorded during June is 39 units (approximately 190 f.c.), there is only a very short period around midday on the brightest sunny days when all activity is inhibited. On cloudy days, *G. pallidipes* are often active throughout the whole day, the degree of activity depending upon the thickness of the clouds; however, this effect is often masked by low temperature and high humidity which depress the activity of the fly.

10. Discussion and conclusions

Fuller & Mossop (1929) observe:

Croveri writing of *G. pallidipes* as far back as 1919, remarked that: 'On sunny days it bites from early dawn up to about 8 a.m. reappearing at 4 p.m. and disappearing at dark. On cloudy days and rainy days it bites during the whole days.' The morning and evening periodicity of the species has been noted by others as well, but it never has to our knowledge been suggested that the insect responds to what might be considered an optimum temperature. We have also observed this periodicity, but it is not a rigid characteristic since biting may proceed through the whole of a normally warm, sunny summer's day. There is a difference, however, as the attacking flies come only at the rate of 1–2 in 5 min. instead of 1–2 in 1 min. Upon extremely hot days, shade temperature 102–104° F. (39–40° C.), *G. pallidipes* is inactive.

Fuller & Mossop carried out their observations in Zululand which is in latitude (approximately) 27° S., and the sun would never be directly overhead. On the other hand, Croveri's observations were carried out in Italian Somaliland, between latitudes 0° and 10° N., where the sun would be directly overhead twice each year. One would expect from the results set out in this paper that *G. pallidipes* would be active throughout the day in Zululand, even at the period of maximal light intensity. Whereas in Somaliland one would not expect to find *G. pallidipes* active around midday (except perhaps in the thickets) near the equinoxes; this is of course assuming the respective temperatures and humidities are about equal.

Preliminary analysis of the data also shows that temperature affects the reaction of *G. pallidipes* to light intensity. At a low temperature, 20° C., they remain active at higher light intensities than when the temperature is 30° C. The effect of temperature is, however, not a simple one, since activity rises with the rising temperature up to 30° C. after which point it falls (see Part 1). Other complicating factors such as humidity and hunger have already been mentioned.

Since this paper was first drafted, I visited *G. pallidipes* areas in Zululand and took the same light intensity apparatus as used in Tanganyika. The mean readings on cloudless middays during 22–24 November 1941 in open country were 38 units (approximately 175 f.c.) and in thorn bush 32 units (approximately 120 f.c.). The maximal light intensity would be somewhat higher than this during the December equinox but considerably lower during the winter months (March to September).

These observations demonstrate that one would not expect to catch *G. pallidipes* in open bush country on bright days, and that the most favourable time is during the evening, providing the air temperature is not too excessive (optimum about 30° C.). It is not, however, possible to carry out tsetse surveys only during the evenings, and the results indicate that one could correct the numbers caught for a constant light intensity, temperature and humidity using the regressions obtained from the correlations. For each rise of 1 unit of light intensity (or 100 % increase in foot-candles) there is a corresponding decrease of 20 % in the *total* (male and female) catch of *G. pallidipes*. Field catches can be corrected on this basis, providing that some flies, preferably more than ten, have been taken in each catching period. Negative catching periods cannot be corrected. When

carrying out tsetse fly surveys the complete failure to catch suggests that the flies are absent from that particular locality. If temperature, humidity and light intensity were recorded at regular intervals these data can be examined and compared with the expected mean activity of *G. pallidipes* as shown in the correlation tables. Surveys carried out in adverse conditions would have to be repeated at more favourable times. The period of time taken for each catching period should be governed by the rate of change of the various climatic factors and the numbers of flies caught, which will depend upon their activity and population. The catching periods should be long enough to take more than ten individuals in each period, yet not sufficiently long for the temperature (wet and dry) to have changed more than 1° C. and the light intensity (as foot-candles) more than ± 50% variation. This is best brought about by recording the climatic factors and catch at short 5 min. intervals and deciding the duration of each 'catching' period when the data are complete, which can be done by combining 2, 3, 4 or more, 5 min. periods together. Such 'catching' periods must of course be equal throughout any one comparable set of observations.

PART 3. THE EFFECTS OF WIND VELOCITY AND BAROMETRIC PRESSURE UPON ACTIVITY

11. Instruments used

The wind velocity was recorded in hundreds of feet per quarter-hour using a Byram's Airmeter. This instrument was checked daily with a standard anemometer, which was set up a few yards away from the catching station; both instruments were placed 5 ft. above the ground-level. The barometric pressure was recorded by a small aneroid, adapted for work in the field and adjusted to the high altitude. The barometric pressure has been recorded as deviations from the mean rather than in actual inches or millimetres of mercury, which might show a constant error.

12. Daily and monthly variation of wind velocity and barometric pressure

During the rains (November to May) there is usually a breeze during the early morning and late evening, and a wind before a squall, while in the early dry season (June to August) there is usually a high wind up to a maximum of 15 m.p.h. during the mornings. This wind, however, usually dies away towards the afternoon, whereas during the late dry season (September to the end of October) there is a strong breeze morning and evening. The average velocity in miles per hour, monthly for 1941 in open country at Old Shinyanga, is given in Table 6. It will be seen

Table 6. Glossina pallidipes *catch against time of day. Outside 'home' environment of the tsetses, namely in a hardpan area. Figures are not 'corrected' for any other factors*

Hour-period (sun-time)	No. of ½ hr. catches	Average *G. pallidipes* per 7½ hr. catch		
		Males	Females	Total
7.00–	28	48·0	15·5	63·5
8.00–	44	64·6	24·5	89·1
9.00–	44	27·2	10·2	37·4
10.00–	44	11·6	7·5	19·1
11.00–	44	8·2	11·6	19·8
12.00–	44	4·1	5·4	9·5
1.00–	44	2·0	11·1	13·1
2.00–	44	4·7	13·5	18·2
3.00–	44	15·0	32·0	47·0
4.00–	44	34·7	43·6	78·3
5.00–	44	44·9	67·3	112·2

that the average is lowest during December and January, and increases up till the end of October, and then decreases in November (commencement of the rains). A cup anemometer was set up in both catching sites, open hardpan and *Euphorbia* thicket, and the wind velocity was measured concurrently with the Old Shinyanga meteorological station over a period of 4 months, January to April 1941. It was found that the wind velocity in the hardpan site was approximately one-quarter, and in the thicket site one-twentieth of that of the meteorological station, which was within 3 miles of both sites.

Unlike temperate regions, the East African tropics show extremely steady barometric pressure, with regular daily and annual oscillations. The barometer falls from about 6 a.m. until 10 a.m. when it rises rapidly until 2 p.m. and then falls until 10 p.m. (East African Standard time). The daily range is on an average 0·10 in. of mercury. The annual variation of the barometer correlates closely with that of wind velocity; barometric pressure is high in January and at its lowest during October, as shown in Table 4.

The only other changes in barometric pressure that are noticeable in the tropics are sudden drops just before a heavy thunderstorm or squall.

13. Activity

The wind was recorded in the field in hundreds of feet per quarter-hour against the catch of male, female and total *Glossina pallidipes*, over a series of observations for several consecutive days each month from September 1940 to August 1941 in both sites. The total (male and female) *G. pallidipes* catch each quarter-hour period is shown arranged against its corresponding wind velocity or deviation from the mean barometric pressure in correlation Tables 10–13; these two sets of readings have been chosen as

being typical of wet and early dry season conditions. The data were collected in the open hardpan site on 14, 18 and 21 February 1941 and on 20 and 21 June 1941, and the logarithms of the catch-plus-one have been correlated with either wind velocity or barometric pressure. These results are shown in Table 14 and none is significant. The logarithm of total *G. pallidipes* catch-plus-one in the thicket site have also been correlated with the wind velocity for various seasonal samples, but all give a similar result to those shown above.

As already mentioned, the wind velocity in the hardpan site was approximately one-quarter that of the meteorological station in the open at Old Shinyanga, and one-twentieth of the latter in the flies' home environmental thickets. The greatest recorded wind velocity in the field at the time of the experiments was 4·73 m.p.h. Fuller & Mossop (1929) record that on extremely windy days one has to seek the shelter of a dense thicket to find *G. pallidipes* active. Their observations were carried out in Zululand where the bush outside the thickets is well spaced and subject to strong moist winds.

The writer has also observed that *G. pallidipes* appear to become more active prior to a thunderstorm; this it was thought might be due to changes in barometric pressure; but so far the data do not support this supposition. It appears that the falling light intensity due to gathering clouds is the most probable explanation.

Table 7. *Average wind velocity per hour monthly for* 1941

Month ...	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Wind (m.p.h.)	1·64	2·43	2·09	2·65	2·42	2·79	3·76	4·20	4·46	4·50	2·23	1·66

The wind velocity is given in miles per hour.

Table 8. *Daily variation of barometric pressure, deviation from mean in inches of mercury*

Time ...	6.0 a.m.	8.0 a.m.	10.0 a.m.	Noon	2.0 p.m.	4.0 p.m.	6.0 p.m.
Inches of mercury ...	−0·006	−0·030	−0·041	−0·014	+0·005	+0·043	+0·031

The mean has been taken over the 12 hr. of daylight.

Table 9. *Monthly variation of barometric pressure, deviation from mean in inches*

Month ...	Jan.	Feb.	Mar.	Apr.	May	June
Inches of mercury ...	+0·033	+0·030	+0·025	+0·018	0·00	−0·020
Month ...	July	Aug.	Sept.	Oct.	Nov.	Dec.
Inches of mercury ...	−0·030	−0·033	−0·034	−0·020	+0·010	+0·030

Table 10. *Wind velocity and catch of* Glossina pallidipes

G. pallidipes catch per quarter-hour in hardpan of Block 10C on 20 and 21 June 1941

Wind velocity in hundreds of feet per quarter-hour

Total (male and female) *G. pallidipes* per quarter-hour	0–20	20–40	40–60	60–80	80–100	100–120	120–140	140–160	160–180	180–200		
11	.	1	.	.	.	.	.	.	.	.	1	+100
10	.	1	1	.	.	.	.	.	.	.	2	+95
9	.	.	.	.	.	.	.	.	.	.	.	+90
8	.	.	.	.	.	.	.	1	.	.	1	+85
7	.	1	.	.	.	.	.	.	.	.	1	+78
6	1	.	.	.	.	.	.	.	.	.	1	+70
5	.	.	.	.	.	1	.	.	.	.	1	+60
4	1	1	2	1	.	.	.	2	.	.	7	+48
3	.	5	2	.	.	.	1	.	.	.	8	+30
2	3	2	2	5	6	2	.	.	.	.	20	0
1	3	5	2	.	3	.	.	.	1	.	14	−30
0	2	7	4	6	.	.	.	2	.	1	22	−48
	10	23	13	12	9	3	1	5	1	1	78	
	+2	+1	0	−1	−2	−3	−4	−5	−6	−7		

Table 11. *Catch of total* Glossina pallidipes *and barometric pressure*

Data taken on 20 and 21 June 1941 in hardpan in Block 10C.

Total *G. pallidipes* per quarter-hour	Barometric pressure (in inches) deviation from mean										
	+0·040 (+0·036 to +0·045)	+0·030 (+0·026 to +0·035)	+0·020 (+0·016 to +0·025)	+0·010 (+0·006 to +0·015)	+0·000 (+0·005 to −0·005)	−0·010 (−0·006 to −0·015)	−0·020 (−0·016 to −0·025)	−0·030 (−0·026 to −0·035)	−0·040 (−0·036 to −0·045)		
11	.	.	1	.	.	.	.	.	.	1	+100
10	.	.	.	.	.	.	1	1	.	2	+95
9	.	.	.	.	.	.	.	.	.	.	+90
8	.	.	.	.	.	.	.	.	1	1	+85
7	.	1	.	.	.	.	.	.	.	1	+78
6	.	1	.	.	.	.	.	.	.	1	+70
5	.	.	.	.	.	1	.	.	.	1	+60
4	2	3	1	.	.	1	.	.	.	7	+48
3	2	1	2	1	.	.	.	1	.	7	+30
2	1	1	3	3	.	.	5	4	4	21	0
1	.	.	.	3	3	1	.	5	.	12	−30
0	1	1	2	4	4	4	3	3	2	24	−48
	6	8	9	11	7	7	9	14	7	78	
	+4	+3	+2	+1	0	−1	−2	−3	−4		

Table 12. *Total* (*male and female*) Glossina pallidipes *catch and wind velocity. February* 1941

G. pallidipes catches on ox on 14, 18 and 21 February 1941

Total *G. pallidipes* per quarter-hour	Wind velocity in hundreds of feet per quarter-hour																
	0–9	10–19	20–29	30–39	40–49	50–59	60–69	70–79	80–89	90–99	100–109	110–119	120–129	130–139	140–149		
9	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	1	+90
8	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+85
7	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+78
6	1	.	1	2	.	.	.	.	.	.	.	.	.	.	.	4	+70
5	.	.	1	1	1	.	.	.	.	.	.	.	.	.	.	3	+60
4	3	1	1	1	.	1	.	.	.	.	.	1	.	.	.	8	+48
3	3	2	.	4	.	.	.	1	1	.	.	.	.	.	1	12	+30
2	4	6	6	4	4	1	1	.	1	.	.	.	.	2	.	29	0
1	2	6	1	2	3	2	.	.	1	.	.	.	.	.	.	17	−30
0	7	7	8	6	7	3	2	.	.	.	1	.	1	.	.	42	−48
	20	23	18	20	15	7	3	1	3	.	1	1	1	2	1	116*	
	+4	+3	+2	+1	0	−1	−2	−3	−4	−5	−6	−7	−8	−9	−10		

* One reading omitted as mistake was made in recording wind value, so total differs by one from that of Table 13.

Table 13. *Catches from hardpan in Block* 10 C, 14, 18 *and* 21 *February* 1941

Catches from stationary ox

Total *G. pallidipes* catch per quarter-hour	Barometric pressure (in inches) deviation from mean										
	−0·036 to −0·045	−0·026 to −0·035	−0·016 to −0·025	−0·006 to −0·015	−0·005 to +0·005	+0·006 to +0·015	+0·016 to +0·025	+0·026 to +0·035	+0·036 to +0·045		
6	1	1	.	.	.	.	.	.	1	3	+70
5	.	1	.	.	.	.	.	.	.	1	+60
4	.	3	1	.	1	.	1	1	.	7	+48
3	1	1	2	3	1	1	2	2	.	13	+30
2	5	6	3	2	.	2	2	9	3	32	0
1	1	5	.	.	2	2	2	1	2	15	−30
0	1	9	3	3	8	5	6	6	5	46	−48
	9	26	9	8	12	10	13	19	11	117	
	+4	+3	+2	+1	0	−1	−2	−3	−4		

Table 14. *Correlation of catch with wind velocity and barometric pressure*

		N	*r*
16–20 February 1941	(*a*) Wind velocity	116	−0·0095
	(*b*) Barometric pressure	117	+0·1354
20 and 21 June 1941	(*a*) Wind velocity	78	−0·0090
	(*b*) Barometric pressure	78	+0·2055

None of these is significant.

14. SUMMARY

1. The methods of catching *Glossina pallidipes* and the statistical methods used are outlined. The flies were taken on stationary oxen, the catch being recorded as total males, females, etc., for every quarter-hour throughout the day, together with the temperature, wet and dry bulb, wind velocity, light intensity, black-bulb thermometer, evaporation rate and other climatic factors. The catches-plus-one have been converted into logarithms and these, as an index of activity, have been correlated with the climatic factors.

Part 1

2. The results of correlating the activity (catch) of *G. pallidipes* with saturation deficit in millibars for different temperature groups are given in Table 1. The following temperatures groups were used; 19–25°, 26 and 27°, 28°, 29°, 30°, 31°, 32°, 33°, 34°, 35° and 36° C. The value of *r* is positive for temperature groups up to 30° C. where no correlation exists, and negative for temperature groups above 30° C. All the coefficients are significant except at 30° C., and all groups are significantly different from their neighbours except the two on each side of temperature group 30° C. The slopes of the regressions of catch on saturation deficit are steepest at the extreme temperatures; the catch increases with the rising saturation deficit below 30° C. and decreases with the rising saturation deficit above 30° C.

3. The same effects are found when the data is separated out into humidity groups, activity increases with rising temperatures up to 25 mb., but decreases with rising temperatures above this humidity.

4. Other correlations are mentioned but not given in detail since their results were very similar to those already described in this paper.

Part 2

5. The methods of measuring light intensity and radiated heat as recorded by a black-bulb thermometer *in vacuo* are given.

6. Tables showing the comparative monthly and daily variations of both light intensity and black-bulb temperature are given for the Old Shinyanga area,

latitude 3° 33′ S., where the observations upon *G. pallidipes* were carried out.

7. Table 4 gives the mean catches of male, female and total *G. pallidipes* for each hour of the day in the 'home' environment. Table 6 gives comparative catches, hourly, from an area outside the tsetses 'home' environment.

8. Correlations of *G. pallidipes* activity with both light intensity and black-bulb temperature, in and outside the tsetses 'home' environment, were negative and highly significant, but those with light intensity were the stronger.

9. Experiments showed that *G. pallidipes* is active after dusk, and that they can perceive light below 3000 Å. and that between 4000 and 6500 Å. They are also attracted to heated surfaces.

10. For each 100% increase of light intensity as measured by foot-candles there is a corresponding decrease of 20% in the total numbers of male and female *G. pallidipes* caught. These data can be used to estimate the probable catch at a given light intensity, and also explain the failure to catch this species under certain conditions.

Part 3

11. Data have been collected on the activity of *G. pallidipes* in relation to wind velocity, both inside and outside the flies' home environment. Wind velocity up to 4·73 m.p.h. was recorded outside the flies' home environment. The correlations of the logarithm of the catch-plus-one with the wind velocity were not significant. The correlation tables for the data obtained outside the flies' home environment are given, together with tables showing the daily and monthly mean wind velocities.

12. Simultaneously observations upon the activity of *G. pallidipes* in relation to barometric pressure were recorded. Barometric pressure has been recorded as deviations from the mean and correlated with the catch-plus-one; none of the correlations is significant.

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APPENDIX 1

Quarter-hour catches of male Glossina pallidipes *during July and October at identical wet- and dry-bulb readings*

Date	Dry	Wet	♂♂	Date	♂♂
16 July 1940	30	20	0	28 Oct. 1940	3
16 July 1940	30	20	3	28 Oct. 1940	0
16 July 1940	30	20	1	24 Oct. 1940	8
16 July 1940	30	20	2	24 Oct. 1940	1
16 July 1940	30	20	2	23 Oct. 1940	0
16 July 1940	30	20	0	23 Oct. 1940	1
16 July 1940	30	20	2	18 Oct. 1940	1
16 July 1940	30	20	2	18 Oct. 1940	1
16 July 1940	30	20	1	18 Oct. 1940	0
19 July 1940	30	20	4	15 Oct. 1940	2
4 July 1940	30	20	0	15 Oct. 1940	3
4 July 1940	30	20	1	15 Oct. 1940	0
4 July 1940	27	20	2	14 Oct. 1940	0
4 July 1940	29	20	1	14 Oct. 1940	0
22 July 1940	32	21	4	11 Oct. 1940	4
22 July 1940	29	19	7	11 Oct. 1940	4
22 July 1940	29	19	5	11 Oct. 1940	4
12 July 1942	25	23	5	10 Oct. 1940	1
16 July 1942 (2)	31	22	1	4 Oct. 1940	3
16 July 1942	30	20	1	4 Oct. 1940	4
16 July 1942	30	20	0	4 Oct. 1940	1
25 July 1942	29½	19	2	4 Oct. 1940	1
25 July 1942	29	19	2	4 Oct. 1940	3
16 July 1942	31	20	1	3 Oct. 1940	1
19 July 1942	30	20	4	15 Oct. 1940	7
19 July 1942	30	17	0	24 Oct. 1940	1
26 obs.			53	26 obs.	54

APPENDIX 2

Correlation tables of log male Glossina pallidipes *catch-plus-one per quarter-hour with saturation deficit at different temperature levels*

	Temp. 19–25° F.									Log of catch-plus-one
	.	.	.	.	.	1	.	.	.	1	0·85
	.	.	.	.	1	.	.	.	1	2	0·78
	.	.	.	1	2	.	1	.	.	4	0·70
	.	.	4	3	1	1	1	.	.	10	0·60
	.	.	2	1	2	.	.	.	.	5	0·48
	.	6	3	.	4	.	.	.	.	13	0·30
	6	13	2	1	1	.	.	.	.	23	0·00
	6	**19**	**11**	**6**	**11**	**2**	**2**	**.**	**1**	**58**	
Sat. def.	0–3	4–7	8–11	12–15	16–19	20–23	24–27	28–31	32–35		

Appendix 2 (*cont.*)

Temp. 26–27° C.

																	Log of catch-plus-one
.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	1·04
.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1·00
.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	0·95
.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	2	0·90
.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	1	.	2	0·85
.	.	.	.	.	.	.	.	.	.	.	.	2	1	1	1	.	5	0·78
.	.	.	.	.	.	1	1	.	.	.	.	1	4	2	1	.	10	0·70
.	.	.	1	.	1	1	.	1	1	.	.	2	.	1	1		9	0·60
.	1	.	.	.	.	1	.	3	2	1	2	3	1	1	.		15	0·48
1	1	1	.	2	1	2	1	4	7	5	1	5	2	1	1		35	0·30
.	1	3	3	2	1	2	2	1	1	1	1	1	.	.	.		19	0·00
1	3	4	4	4	3	7	4	9	11	7	7	19	6	6	3		98	

Sat.	2	4	6	8	10	12	14	16	18	20	22	24	26	28	30	32
def.	3	5	7	9	11	13	15	17	19	21	23	25	27	29	31	33

Temp. 28° C.

															Log of catch-plus-one
.	.	.	.	.	.	.	.	.	1	1	.	.	.	.	2	1·00
.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	1	0·95
.	.	.	.	.	.	.	.	1	.	.	.	1	.	.	2	0·90
.	.	.	.	.	.	1	1	2	3	1	2	.	.	.	10	0·85
.	.	.	.	.	.	.	.	3	.	1	2	.	.	.	6	0·78
.	.	1	1	.	.	1	1	4	1	4	5	1	1	.	20	0·70
.	4	1	1	1	.	3	2	6	7	2	4	2	.	.	33	0·60
.	1	3	1	1	2	2	6	3	8	11	8	2	.	.	48	0·48
.	2	2	1	5	2	3	7	4	6	6	3	1	.	.	42	0·30
3	7	7	3	4	2	3	4	10	9	6	1	1	.	1	61	0·00
3	14	14	7	11	6	13	21	33	35	33	25	8	1	1	225	

Sat.	6	8	10	12	14	16	18	20	22	24	26	28	30	32	34
def.	7	9	11	13	15	17	19	21	23	25	27	29	31	33	35

Temp. 29° C.

															Log of catch-plus-one
.	.	.	.	.	.	.	.	1	1	.	.	.	.	.	2	1·23
.	.	.	.	.	.	.	.	1	2	.	.	.	.	.	3	1·20
.	.	.	.	.	.	.	.	1	.	.	.	.	.	1	2	1·18
.	.	.	.	.	.	.	.	2	.	.	.	.	2	.	4	1·15
.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	2	1·11
.	.	.	.	.	.	.	.	.	.	.	.	.	2	2	4	1·08
.	.	.	.	.	.	.	.	2	.	.	.	.	1	.	3	1·04
.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	1	1·00
1	.	.	.	.	.	1	.	3	.	1	2	.	.	.	8	0·95
.	.	1	.	.	.	.	.	4	2	2	2	.	2	1	14	0·90
.	.	.	.	.	.	1	1	4	1	.	.	.	.	.	7	0·85
.	.	.	.	1	.	1	4	6	5	5	.	1	2	1	26	0·78
1	1	.	.	1	.	1	9	7	4	3	.	.	2	2	31	0·70
1	1	.	.	2	3	6	10	14	8	4	.	.	1	4	54	0·60
3	3	1	1	1	4	6	12	19	12	8	2	.	1	4	77	0·48
2	2	1	2	2	8	8	10	19	16	8	.	3	4	2	87	0·30
3	3	.	5	1	5	4	11	22	12	5	1	1	1	1	75	0·00
11	10	3	8	8	20	28	57	108	63	36	7	5	18	18	400	

Sat.	8	10	12	14	16	18	20	22	24	26	28	30	32	34	36
def.	9	11	13	15	17	19	21	23	25	27	29	31	33	35	37

Appendix 2 (*cont.*)

Temp. 30° C.

																Log of catch-plus-one
.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	1	1·18
.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	1	1·15
.	.	.	.	.	.	2	.	.	1	1	.	.	.	.	4	1·11
.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	1	1·08
.	.	.	.	.	.	.	.	1	2	.	.	.	.	.	3	1·04
.	.	.	.	.	.	1	.	.	3	1	.	.	1	.	6	1·00
.	.	.	.	.	.	.	.	.	3	1	.	.	.	.	4	0·95
.	.	.	.	.	.	.	.	.	3	3	.	.	.	.	6	0·90
.	.	.	.	.	.	.	.	2	7	5	1	.	.	.	15	0·85
1	.	1	.	1	2	3	1	1	2	4	.	3	1	.	20	0·78
.	1	.	.	1	1	1	.	3	11	9	2	5	2	.	36	0·70
.	1	.	1	.	1	1	.	2	21	10	2	1	5	.	45	0·60
1	.	1	1	.	3	4	1	3	24	24	3	5	8	2	80	0·48
.	1	.	3	1	2	9	.	3	21	16	9	5	5	2	77	0·30
1	.	1	2	1	1	6	1	3	25	11	4	7	6	1	70	0·00
3	**3**	**3**	**7**	**4**	**10**	**29**	**3**	**18**	**124**	**85**	**21**	**26**	**28**	**5**	**369**	
Sat.	8	10	12	14	16	18	20	22	24	26	28	30	32	34	36	
def.	9	11	13	15	17	19	21	23	25	27	29	31	33	35	37	

Temp. 31° C.

															Log of catch-plus-one
.	.	.	.	1	.	1	.	.	.	.	.	.	.	2	1·20
.	.	.	.	1	.	1	.	.	.	.	.	.	.	2	1·18
.	.	.	.	1	1	1	.	.	.	.	.	.	.	3	1·15
.	.	.	.	.	.	.	1	.	.	.	.	.	.	1	1·11
.	.	.	.	.	2	.	2	.	.	.	.	.	.	4	1·04
.	.	.	.	2	1	.	2	.	.	.	.	.	.	5	1·00
1	.	.	1	.	2	1	1	.	.	.	.	.	.	6	0·95
.	.	1	1	2	1	4	3	1	.	.	.	.	.	13	0·90
.	1	1	1	.	.	.	8	1	1	.	.	.	.	13	0·85
.	.	.	1	5	.	2	3	.	3	1	.	.	.	15	0·78
.	1	.	4	1	1	1	8	.	5	.	.	.	.	21	0·70
.	1	.	1	2	2	6	18	1	9	3	.	.	.	43	0·60
.	1	.	2	1	7	8	13	4	17	4	1	.	.	60	0·48
.	.	.	.	1	2	9	17	7	18	6	1	2	.	61	0·30
.	.	.	.	1	2	8	12	8	14	3	5	1	1	55	0·00
1	**4**	**2**	**11**	**18**	**21**	**42**	**88**	**22**	**67**	**17**	**7**	**3**	**1**	**304**	
Sat.	14	16	18	20	22	24	26	28	30	32	34	36	38	40	
def.	15	17	19	21	23	25	27	29	31	33	35	37	39	41	

Temp. 32° C.

														Log of catch-plus-one
.	.	.	.	.	1	1	.	2	2	.	.	.	.	6	0·95
.	.	.	1	1	.	1	.	3	1	.	.	.	.	7	0·90
.	.	.	.	2	.	.	2	3	5	2	.	.	.	14	0·85
1	.	.	.	2	.	1	1	5	4	3	.	.	.	17	0·78
1	.	.	.	2	.	.	4	9	7	3	.	.	.	26	0·70
.	.	.	.	2	.	2	7	8	6	1	2	.	.	28	0·60
.	.	.	.	1	2	1	8	19	19	7	3	.	.	60	0·48
.	.	.	.	2	.	7	12	16	21	16	6	1	.	81	0·30
.	.	.	.	2	.	.	4	29	33	14	15	3	3	103	0·00
2	**0**	**0**	**1**	**14**	**3**	**13**	**38**	**94**	**98**	**46**	**26**	**4**	**3**	**342**	
Sat.	14	16	18	20	22	24	26	28	30	32	34	36	38	40	
def.	15	17	19	21	23	25	27	29	31	33	35	37	39	41	

Appendix 2 (*cont.*)

Temp. 33° C.

									Log of catch-plus-one
1	.	.	.	.	.	.	.	1	0·95
1	1	.	.	.	.	.	.	2	0·90
.	.	.	.	.	.	.	.	0	0·85
3	1	1	.	.	.	.	.	5	0·78
2	.	3	2	.	.	.	.	7	0·70
1	5	.	3	1	.	.	.	10	0·60
4	5	3	3	1	1	.	.	17	0·48
1	5	4	6	5	4	1	.	26	0·30
.	.	8	10	8	7	5	8	46	0·00
13	**17**	**19**	**24**	**15**	**12**	**6**	**8**	**114**	
Sat. def. 26, 27	28, 29	30, 31	32, 33	34, 35	36, 37	38, 39	40, 41		

Temp. 34° C.

																Log of catch-plus-one
1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1·00
.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	0	0·95
.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	1	0·90
.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	0	0·85
.	.	.	.	.	1	.	1	.	.	.	.	.	.	.	.	2	0·78
.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	1	0·70
.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	.	2	0·60
.	.	.	.	.	1	.	1	.	1	2	1	2	1	.	.	9	0·48
.	.	.	.	.	.	.	.	.	.	.	1	5	3	2	2	13	0·30
.	.	.	.	.	.	.	.	.	1	.	3	6	12	1	4	27	0·00
1	**0**	**0**	**0**	**0**	**3**	**1**	**2**	**0**	**2**	**2**	**5**	**13**	**17**	**4**	**6**	**56**	
Sat. def.	10	12	14	16	18	20	22	24	26	28	30	32	34	36	38	40	
	11	13	15	17	19	21	23	25	27	29	31	33	35	37	39	41	

Temp. 35 and 36° C.

											Log of catch-plus-one
1	.	.	.	.	.	.	.	.	.	.	1	0·70
1	2	1	.	.	.	.	.	.	.	.	4	0·60
.	1	2	2	1	1	1	.	.	.	.	8	0·48
.	.	.	1	1	3	2	4	.	.	.	11	0·30
.	.	.	.	.	1	1	2	4	5	3	16	0·00
2	**3**	**3**	**3**	**2**	**5**	**4**	**6**	**4**	**5**	**3**	**40**	
Sat. def. 24, 25	26, 27	28, 29	30, 31	32, 33	34, 35	36, 37	38, 39	40, 41	42, 43	44, 45		

REVIEWS

THE JOURNAL OF ECOLOGY

(Vol. 35, Nos. 1 and 2, 1947)

The two numbers for the year 1947 were published together in a single volume of 310 pages, containing twelve original articles, five short reviews, notices of papers of ecological interest, and three further parts of the *Biological Flora*; namely accounts of the two species of *Melandrium* by H. G. Baker, of *Suaeda maritima* and *S. fruticosa* by V. J. Chapman.

In his Presidential address to the Society, 'Pattern and process in the plant community', Dr Watt presents us with a fascinating picture of the complex cyclic phenomena of synthesis and degradation which give the key to understanding the shifting mosaic pattern of many types of plant community, not excepting some which can be regarded as climax types.

African vegetation is dealt with in two articles, one is by H. K. Airy Shaw upon Angola, familiar to botanists as the home of *Welwitschia*, the other is the posthumous publication of G. Milne's 'A soil reconnaissance journey through parts of Tanganyika Territory, December 1935 to February 1936'. It is a masterful presentation of Milne's comprehension of soil-vegetation relationships, and admirably serves the purpose of a memorial to his pioneer work.

J. Grainger, in his paper 'Nutrition and flowering of water plants', seeks to establish variation in carbohydrate economy as the factor controlling flowering, and R. W. Butcher extends his studies of the ecology of rivers by an article upon the algae of river waters through the zones of heavily enrichment with organic matter, and of successive depletion of this organic content. F. T. Walker of the Scottish Seaweed Research Association gives an account of a spring-grab and viewing box used in sublittoral sea-weed survey, and this is followed by consideration of the results of sea-weed survey, on the Orkney coast in two areas: the first at Scapa Flow, and the second at the Bay of Firth.

Applied ecological studies upon the yield, botanical and chemical composition of natural hill herbage under manuring, controlled grazing and hay conditions, are reported upon by W. E. J. Milton and R. O. Davies, who have been experimenting on hill pasture in the Aberystwyth district of Wales.

Dr C. Regel, formerly at the Botanic Gardens in Kaunas, writes from his considerable experiences of the region of White Russia a short review of the bogs and swamps of that region, now in process of drainage and exploitation. Attention is directed to north-west Ireland by a paper upon the vegetation of Carrowkeel, a dissected carboniferous limestone hill in County Sligo. D. A. Webb describes many ecological features in this locality of exceptionally high rainfall and curious topography, particularly the anomalous sparcity of calcicole species and the phenomenon of the growth of acidic peat directly upon the flat limestone surface. F. B. Hora describes the soil pH range of a number of plants which grow on the mountain cliffs in the Cader Idris area of north Wales, and relates the results to the differences in geological character of the parent rocks.

An article by H. Boyko discusses the role of plants as quantitative climate indicators and expounds the 'geo-ecological law of distribution'—that 'The specific topographical distribution (micro-distribution) of an ecotypic plant species or of a plant community is a parallel function of its general geographical distribution (macro-distribution), since both are determined by the same ecological amplitudes'.

We welcome finally an article by Prof. Tansley in which he traces the early stages through which the modern study of ecology has been built up in this country: no one is in so good a position to assess the nature of this development, and no one could present it more precisely.

(Vol. 36, No. 1, 1948)

This part, which contains 236 pages, includes nine original papers of which the first is the important article upon tropical soil-vegetation catenas and mosaics, the outcome of the work of C. G. T. Morison, A. C. Hoyle and J. F. Hope-Simpson, upon the Oxford expedition to the south-western part of the Anglo-Egyptian Sudan. Dr Picki-Sermolli, of the University of Florence, in a short paper recommends a 'maturity index' as a useful part of the statistical investigation of plant communities. A comparison is made by R. Scott Russell of the effects of the Arctic climate of Jan Mayen, and of the high mountain climate of the Karakoram upon the carbohydrate content of the leaves of a species, *Oxyria digyna*, which grows in both places.

H. G. Baker describes the analysis he has made of the processes involved in the natural hybridization in Britain between the two campions *Melandrium album* and *M. dioicum*, and discusses the present and future status of campion populations in different parts of the British Isles. A survey of the Rockland-Caxton level of the Norfolk Broads by Miss J. M. Lambert discloses the dependence of vegetation upon the more or less buried structure of the river-valleys, and especially upon the localization of peat and clay deposited during a period of marine transgression. J. Rishbeth reports the results of the observation of several years upon the flora of walls in Cambridge, Ely and the villages of that district, disclosing very simple and striking relationships to wall-material, age, aspect, and rain-water drainage, and presenting small-scale cyclic succession in the moss-cover. The nature of the population of buried viable seeds in the surface layer of pasture soils is considered in a paper by S. S. Champness and K. Morris of the Stratford-on-Avon Grassland Improvement Station, on the basis of sampling from a big range of pasture-types upon different soils. Dr Seifert's article 'What means this drought?' informally but forcefully suggests that there

appears to be evidence that we are now experiencing one of those climatic shifts which in the past have affected European vegetation, and the agricultural and social pattern of our existence, and in the face of the severity of the 1947 summer drought, recommends that we make sound plans based upon ecological knowledge to meet its recurrence.

In the Reviews Prof. Tansley discusses the implications of the recent work of Crocker and Wood upon the factors controlling South Australian vegetation communities; there is a note of the new vegetation-soil map of North Rhodesia and of Miss Colvin's book on 'Land and landscape'. There follows a list of papers of ecological interest.

Reports are given of the summer excursion of the Society at Bangor in 1947; of the London meeting in June 1947 which was addressed by Prof. Osvald of Uppsala; and of the annual winter meeting at Bristol held in January 1948.

The *Biological Flora* is represented by R. A. Lewin's account of the genus *Sonchus*, and the two British sow-thistles in the genus, *S. oleraceus* L. and *S. asper* (L.) Hill: both are of great economic and botanical interest and are found throughout the British Isles.

H. GODWIN

MALTHUS

(*a*) **Fairfield Osborn (1948).** *Our Plundered Planet.* 217 pp. Little, Brown and Co. Price $ 2.50. [This book is being issued also in England, by Faber and Faber Ltd.]

This book is a primer in the art of becoming a responsible denizen of the Earth. It is simply written, so that even an adult who left school twenty years ago could grasp the meaning, and it should be as much 'required reading' as the *Highway Code* and *Everybody's Guide to National Insurance*. Indeed, it should be the preface to these vital publications.

Mr Osborn's tale is a plain one, namely, the despoliation of the planet by the human species which, looking forth in the dim past as a relatively weak creature of generalized rather than specialized evolution, developed its wits and came to have an increasing power over and influence on its environment. As power has increased numbers have risen to such a pitch that once-fearful and furtive man has become a plague on the planet which he and his ancestors have been plundering at a geometrically increasing rate. The 2000 million mark has been passed and there is scarcely sufficient food-producing acreage to keep the species going. This difficulty could be overcome if only the population would remain static, but this it will not do, and Malthus—at whom there was so much carping in the inter-war period—is now back as an up-to-date prophet. We know quite well that as new food-producing areas are brought into being, the population will increase till it presses against the ceiling again. It does not matter that Malthusian theory does not apply to Britain, France and Sweden; it does apply in Asia, Africa and parts of America, and now, an increasing world population is faced with an environment which has been progressively impoverished. The tailing-off of the curve is too far ahead.

Agriculture as an art has played a losing battle. As soon as a balanced, conserving husbandry has been developed by small peoples in fertile valleys, their numbers have increased so that the forested slopes have been attacked to create new land, with the inevitable results of erosion, destruction and impoverishment. That was an early story, to be read in China and the Mediterranean Basin. A more recent story is the exploitation of new lands to provide food and raw materials for a far-distant population, to be read in America, Australia, South Africa and New Zealand. It is continuing. A third fundamental strife has been going on all the time almost everywhere and is insufficiently realized, probably because we tend romantically to back the wrong side. The Shepherd Kings and Abraham, the 23rd Psalm, the desert Bedouin, the classical goatherd, the cowboy of the ranges, the Australian pastoralist, the Masai spearman who lives on blood and milk—all these are in our religion and romance, a factor in our intellectual environment; yet extended, extractive pastoralism which kills forest, prevents regeneration and solidly overgrazes, has been the most insidious destructive agent on the planet. It is going on now, but American cattle interests and British hill-sheep farmers can always be assured of sympathy before censure.

It is gradually becoming apparent that agriculture must be conducted with a much more biological approach than has been common heretofore. The ecologist must come off his Olympian perch and get his hands—and his head—into the muck of the farm. His possible contribution to world agriculture has been neglected by himself as well as by the rest of men.

Mr Osborn exhorts us to conserve our planet, and this we could do, no doubt. The reader of this sincere book feels that the author is still hopeful that man will put his garden in order, but the reviewer thinks that Mr Osborn glosses over one cardinal factor in man's make-up, his political quality, unique in nature. We see quite well the necessity for reducing—or certainly not increasing—the world population of human beings. Yet every government seems convinced that its own population must not decrease and is afraid lest it may. Increase will, in fact, continue; and in the reviewer's opinion, technology and conservation will not catch up. The plague on the planet will eat itself out.

F. FRASER DARLING

(*b*) **William Vogt (1948).** *Road to Survival.* 335 pp. and 8 text-figures. William Sloane Associates, Inc., 119 West 57th Street, New York, N.Y. Price $ 4.00. [This book is being issued also in England, by Victor Gollancz Ltd.]

Book 4 of Thomas Malthus's monograph on population was entitled: 'Of our future prospects respecting the removal or mitigation of the evils arising from the principle of population.' This might just as well do as a title of Mr Vogt's book. He takes a poor view of these future prospects, unless human beings learn to treat the land and water and the natural resources they support with respect, and also to limit population growth by

means of birth control. We have had books on soil erosion, on economic systems, on cycles of civilization, on population problems, on ecology. This is the first attempt to treat the whole of this grave subject on an ecological basis, for it differs from Mr Osborn's book reviewed above, in that although both authors bring out the vital interaction between over-exploitation of material resources and the increase of population, Mr Vogt sees that technical improvements in land and water management alone will only delay the approaching crisis, and that conscious limitation of the whole human population will alone enable the equation ultimately to be balanced.

The author is among other things a bird ecologist, and at one period carried out a study of the conservation of guano birds on the coast of western South America (I still possess a postcard from him with the classical message: 'My job here is to augment the increment of excrement'!). Later on he gained a great deal of experience of the tougher aspects of land conservation (and exploitation), in his position as chief of the Conservation Section of the Pan-American Union. This first-hand knowledge makes the seventh chapter, on South America, particularly impressive. Of Venezuela, he had already written in 1946: 'The very difficulty of reaching a balanced human ecology makes it imperative not to postpone action'. In the present book Mr Vogt pours out a torrent of facts and energy—'his rollrock highroad roaring down'—and if his style is occasionally purple ('man rapidly increased his command of nature and through a highly skewed development of this command, spawned a vast new school of limiting factors') it is at any rate a fairly royal purple.

His chief message, documented five times over from the different continents, is that man is outrunning his means of subsistence, and yet, through medical and other conditions, letting the steam valve off population control to make an alarming further increase. Even allowing for the slackening of the increase (caused by lower birth-rates) in some of the more highly developed countries, and even if we accept Pearl's tentative fitting of a logistic curve to world population which shows it levelling off by the year 2100 to something like 2645 million bodies, the equation is an exceedingly nasty one to contemplate. Pearson and Harper's 1945 figures, which Mr Vogt considers the most reliable, suggest that the food-growing lands of the whole world are about 2,600,000,000 acres, i.e. between one and two acres per capita; but of this acreage only about a fifth, they say, is good food-growing land. The acreage is now shrinking yearly, and the population increasing. Decrease of white men may at first only accentuate the technical poverty of the other races.

Considerable space is given to a peculiarity of man's population problem, distinct from those of animals: his increasing desire for things and energy (of all kinds) with which to enjoy them. This is usually referred to as man's 'needs', but part of it can be called 'greeds' and much of the rest would be less needed perhaps if people realized the heavy pressure on the world's resources that it has brought about. 'In the time of the Incas...five or six acres could probably support an entire family; to-day they would not buy a family car.' He does not omit to castigate heavily the American high standard of material life, which he regards as an unjustifiable overdraft on the future: 'By the use of the machine, by exploitation of the world's resources on a purely extractive basis, we have postponed the meeting at the ecological judgement seat.' But of course most other countries would go the same way if they could, and the United States is, after all, helping Western Europe to postpone a much earlier meeting there.

To every head of population we must therefore add a coefficient of need or greed, that depends on cultural and technical levels of civilization. From the point of view of a population ecologist the word 'culture' has a slightly ambiguous sound, reminding us also of the bacterial colony reaching saturation on an agar plate!

It might perhaps be inferred from what I have said that this is a bad-tempered book, or that the author just has a bee in his bonnet, or that he is an ascetic, or that he exaggerates the difficulties ahead of mankind even if wars remain comparatively cold or cease. On the contrary, it is essentially not a gloomy book; it is full of challenging energy and desire to see action taken that could be taken; and it is written by an ecologically-minded and also practical man of first-rate intelligence. Anyone who asks: 'What has all this to do with the learned world of animal ecologists?' can find part of the answer in the previous number of this *Journal*, which contains too fairly abstract papers that discuss respectively the dynamics of natural population increase, and the meaning and significance of productivity in ecosystems. They deal with beetles and fresh-water fish and chironomid flies and soil animals, Vogt with human beings. *We* are the beetles and grain is scarce. I think both these ecological papers would have interested 'that clear-sighted English clergyman, Thomas Robert Malthus', who incidentally remarked at the end of his own book that 'it is hoped that the general result of the inquiry is such as not to make us give up the improvement of human society in despair'.

Road to Survival is easy to read; its story too grave to be depressing; it is conveniently documented; and it marks a sharp stage in the application and synthesis of ecological concepts in human affairs. It has a very full index, which equals in startling range of subject-matter my favourite index entries (which are in Lotka's *Elements of Physical Biology*, e.g. 'Verbal problems, Verhulst-Pearl law, Vestal flame, Vicious circles, Vital processes, Vital force, Volcanic discharges, Voluntary action and determinism'). Vogt has similar matings of different components of the vast world scene: as 'Krakatoa volcano, as example of succession of subclimaxes; Ku Klux Klan, and standard of living in the south;—Nitrogen; Non-Aristotelian formulation;—Pizarro; Plagues, grasshopper'.

I like the quoted comment by Christopher Morley, who said: 'This book will give you some of the most valuable anxiety you ever had.' In the ecologist, this anxiety will be tempered by a profound curiosity to know, or a desire to predict, how the human situation will develop. A fairly big oscillation in numbers is, we know, already inherent in the white populations of the world. It seems likely that similar ones will occur in other races, though perhaps more caused by increases in mortality than by deliberate control of births. Before then there may be a slight raising of the *average* standards of life (to the detriment of the more highly developed populations), followed by an

increasing, though very patchily distributed, poverty in material things, during which many paradoxical uses of natural resources will be noticed. It is probable that catastrophic mortality, such as atom-bomb wars and influenza pandemics, will play a much smaller part in determining the structure and density of the human population than is usually imagined, though they may have a perceptible influence in delaying some processes and concentrating into relatively short periods mortalities (such as those from malnutrition) normally spread out over a generation. There will be enormous efforts by the technically advanced countries to 'buy time', i.e. prevent the run-off of water and soil, breed economically growing crops, remove (by drastic poisoning and other means) all possible competitors in the shape of pests, develop marine resources on a very much bigger plan, seek new pockets of mineral resource and stored organic power and canalize atomic energy, and prevent social and industrial waste. But it is on the population question itself that the future really hangs. Here we find a good deal of divergent opinion, and a great many questions that depend less on scientific research and technical planning, than upon social and religious attitudes. Some beliefs, for instance in eternity and other worlds, may make arguments purely from terrestrial conservation inconclusive to the believers. But with all such limitations, there is emerging to view, with books like Mr Vogt's, a picture of human ecology that needs the impartial study of trained animal ecologists.

CHARLES ELTON

NOTICES OF PUBLICATIONS ON THE ANIMAL ECOLOGY OF THE BRITISH ISLES

This series of notices covers most of the significant work dealing with the ecology of the British fauna published in British journals and reports. Readers can aid the work greatly by pointing out omissions and sending reprints of papers and reports to the Editor, *Journal of Animal Ecology*, Bureau of Animal Population, Department of Zoological Field Studies, 91 Banbury Road, Oxford.

Duplicate copies of these notices can be obtained separately in stiff covers (printed on one side of the page to allow them to be cut out for pasting on index cards) from the Cambridge University Press, Bentley House, 200 Euston Road, N.W. 1, or through a bookseller, price 3*s.* 6*d.* per annum post free (in two sets, May and November). Back numbers are available at half price.

Selection and abstracting has been done voluntarily by H. F. Barnes, A. C. Evans, R. S. Fitter, E. M. O. Laurie, C. Matheson, E. Nelmes, W. S. Richards, M. R. Shorten and H. N. Southern; checking by B. M. Hobby.

Within each section the groups are arranged in alphabetical order. Papers dealing with technical methods are dealt with in the appropriate sections.

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1. ECOLOGICAL SURVEYS AND THE RELATIONS OF ANIMALS TO HABITAT CONDITIONS

(*a*) Marine and brackish

Crisp, D. J. & Chipperfield, P. N. J. (1948). 'Occurrence of *Elminius modestus* (Darwin) in British waters.' Nature, Lond. 161: 64.

Records for this immigrant barnacle suggest that it is mainly confined to the south and east coasts of Britain where it occurs intertidally and at depths down to 5 fathoms in habitats similar to that which it occupies in New Zealand. The present distribution does not indicate a recent dissemination but appears to be that of a well-established species. It is possible that its presence has not been recognized for some years. It has a longer breeding than any other barnacle in British waters, and two complete generations may occur in one summer.

(*b*) Fresh water

Gray, E. (1948). 'Ciliate protozoan fauna of soil and inland waters.' Nature, Lond. 161: 854–5.

It is suggested that water ciliates are identical with those of the soil.

Harrison, J. L. (1945). '[The Survey of Bookham Common. Third year.] The water snails of Isle of Wight and Upper Eastern Ponds.' Lond. Nat. No. 24, for 1944: 22–3.

Forty-three samples produced eleven species of snails.

Hickin, N. E. (1947). 'Larvae of the British Trichoptera, 23.' Proc. R. Ent. Soc. Lond. A, 22: 114–17.

Description of the larva of *Plectrocnemia conspersa* (Polycentropidae).

Hickin, N. E. (1947). 'Larvae of the British Trichoptera. 24.' Proc. R. Ent. Soc. Lond. A, 23: 12–13.

Description of the larva of *Limnophilus extricatus* (Limnophilidae).

Hinton, H. E. (1947). 'On the reduction of functional spiracles in the aquatic larvae of the Holometabola, with notes on the moulting process of spiracles.' Trans. R. Ent. Soc. Lond. 98: 449–73.

London Natural History Society (1945). 'The survey of Bookham Common. Third Year.' Lond. Nat. No. 24, for 1944: 15–35. (Also as Lond. Nat. Repr. No. 33).

An introductory paper on the eight ponds on the common and their vegetation, by C. P. Castell (pp. 15–22), is followed by an account by J. L. Harrison (pp. 22–3) of an investigation of the relative numbers of 11 water snails in two ponds at different times of the year, notes by R. M. Payne (pp. 23–31) on the dragonflies at each of seven ponds and two streams during 1942–4 and the status of the 16 species noted, of which five are recorded for the first time, and seasonal observations, also by R. M. Payne (pp. 31–5) on the beetles associated with the marginal vegetational areas of three ponds on each of eleven monthly visits during 1943. The survey base map is again included.

Payne, R. M. (1945). '[The Survey of Bookham Common. Third year.] Notes on the distribution of dragonflies on Bookham Common.' Lond. Nat. No. 24, for 1944: 23–31.

Discusses the Odonata of six areas of surface water on the Common, and lists 16 species for the survey area.

Stewart, R. N. (1948). 'Spawning sea trout: some observation on two Scottish burns.' Salm. Trout Mag. No. 123: 121–4.

An account of the spawning behaviour of sea-trout based on observations made under good conditions. The interpretation of various activities is different from that given by other observers.

(*c*) Land

Bayes, C. S. (1944). '[The Epping Forest Survey. Second year.] A historical sketch of Epping Forest.' Lond. Nat. for 1943: 32–43.

Deals with the biotic effect of man on the Forest since the Ice Age.

Beirne, B. P. (1947). 'The origin and history of the British Macro-Lepidoptera.' Trans. R. Ent. Soc. Lond. 98: 275–372.

Answers the questions how and why each species first became established in the British Isles, why each species has its own particular type of distribution, why many species are represented by local races and gives information concerning the histories of the species subsequent to their establishments.

Beirne, B. P. (1948). 'Notes on the origin and history of the British insect fauna.' Proc. R. Ent. Soc. Lond. A, 23: 1–8.

Further examples of insects whose distributions, habits or variation confirm or amplify certain of the conclusions reached in earlier paper (1947, Trans. R. Ent. Soc. Lond. 98: 273–372).

Bonner, A. [1946]. 'The lesser whitethroat *Sylvia curruca curruca* (L.): some observations on its distribution in Leicestershire.' Leicestershire and Rutland County Rep. on Wild Birds for 1945: 12–16.

Discusses four ecological factors affecting the bird's distribution: habitat, altitude, presence of still or running water, and geology; and concludes that the two most important are the sort of habitat typified by grassy lanes and bridle tracks and a subsoil of boulder clay.

Broadbent, L. & Hull, R. (1947). 'Aphides in root clamps.' J. Minist. Agric. 54: 319–22.

The peach-potato aphis (*Myzus persicae*), overwintering in clamps is protected against severe frosts, feeds and multiplies on the young shoots around the mangold crowns and may build up large populations which can carry plant viruses from the clamp to growing plants. The tulip aphis (*Hyperomyzus staphyleae*) and the shallot aphis (*Myzus ascalonicus*) were also found in clamps.

Carrington, L. I., Castell, C. P. & Wilton, A. R. (1944). '[The Survey of Bookham Common. Second year.] Somepreliminary notes on the birds of Bookham Common.' Lond. Nat. for 1943: 23–9.

Includes two maps showing the song-posts of four resident and six migrant species on the common.

Castell, C. P. (1943). 'The Survey of Bookham Common. First year. Some preliminary observations on the base map and topography.' Lond. Nat. for 1942: 28–31.

Introduction to the ecological survey of Bookham Common, Surrey, begun in 1942 by the Ecological Section of the London Natural History Society.

C[astell], C. P. (1944). 'The Survey of Limpsfield Common. Seventh year. Bibliography, 1937–1943.' Lond. Nat. for 1943: 30–1.

Lists all papers published in the *London Naturalist* on the ecological survey of Limpsfield Common, Surrey, carried out by the Ecological Section of the London Natural History Society during 1936–40; with an analysis by subjects.

Collinge, W. E. (1947). 'Further notes on the terrestrial Isopoda.' Northw. Nat. 22: 84–7.

Contains an account of an experiment with *Oniscus asellus* over a period of three years in which there was an increase in successive broods in the percentage of females and the amount of yolk in the ova, as well as a marked increase in the size of the females, when well-fed females kept at an average temperature of 60° F. were mated with starved males; a record of a new variety of *Armadillidium vulgare* (var. *nigra*) from Glamorgan; a record of *Trichoniscus viridus* from County Mayo and another, apparently the first, from County Antrim; and additional records of *Platyarthrus hoffmannseggii* from Counties Antrim, Down and Kerry.

Easton, A. M. (1946). 'The Survey of Bookham Common. Fourth year. An annotated list of the Rhynchophora of Bookham Common.' Lond. Nat. No. 25, for 1945: 56–63.

Details of the habitats of the weevils of the Common.

F[itter, R. S. R.] (1941). 'Special species for 1940. [Sand-martin. *Riparia r. riparia* (L.).]' Lond. Bird Rep. for 1940: 16–18.

Relates the distribution of the sand-martin in the London Area to the presence of artificial cliffs or banks in certain types of sub-soil. The bird is found only on sand, gravel, brick-earth and alluvium and not at all on clay or chalk. One site in a natural sand-bank is cited, and several in wholly artificial holes in brick or concrete structures.

Fitter, R. S. R. (1941). 'The Survey of Limpsfield Common. Fourth year. Mammals, reptiles and amphibians, 1938–40.' Lond. Nat. for 1940: 18–19.

Additions to list published in 1938.

Harrison, J. L. (1943). 'The Survey of Limpsfield Common. Sixth year. Rabbits on Limpsfield Common.' Lond. Nat. for 1942: 40–1.

Maps the distribution of *Oryctolagus cuniculus* burrows on the common.

Harrison, J. L. (1943). '[The Survey of Limpsfield Common. Sixth year.] Grasshoppers on Limpsfield Common.' Lond. Nat. for 1942: 41–2.

Three species of short-horned grasshoppers (*Acrididae*) were found on the common; details of habitat are given.

Harvey, J. H. (1943). '[The Survey of Bookham Common. First year.] Bookham Common: a short history.' Lond. Nat. for 1942: 32–40.

Summarizes the biotic effect of man on the common since the eleventh century; a map illustrates the enclosures.

Jary, S. G., Rolfe, S. W. H. & Carpenter, K. (1948). 'The leek moth.' J. Minist. Agric. 54: 563–9.

Three generations, possibly a fourth in exceptional years. Hibernation as a moth. Eggs first found during mid-April. Restricted to coastal areas in east and south-east England.

Kaufmann, R. R. V. (1947). 'A contribution to the history of the longicorn Coleoptera of Cheshire.' Northw. Nat. 22: 95–101.

This annotated list of longicorn beetles in Cheshire is based on the literature, museum specimens and correspondence, and brings the information available up to date. No other collated list has appeared for 16 years.

London Natural History Society (1943). 'The survey of Bookham Common. First Year.' Lond. Nat. for 1942: 28–40.

This preliminary report contains an account of the area in Surrey to be surveyed and notes on the construction and use of a specially prepared base map with a superimposed grid, which is also given, all by C. P. Castell (pp. 28–31), and an account of the history of the common by J. H. Harvey (pp. 32–40).

London Natural History Society (1944). 'The survey of Bookham Common. Second Year.' Lond. Nat. for 1943: 22–9. (Also as Lond. Nat. Repr. No. 29.)

This report comprises a preliminary list, compiled by L. I. Carrington, C. P. Castell and A. R. Wilton, of 80 birds recorded in the area during the previous 10 years. Of these, 76 were observed in 1942–3, and observations on their distribution, abundance, status and habits are given, with maps showing the position of song-posts of four resident and six migrant birds in 1943.

London Natural History Society, Chingford Branch Council (1943). 'The Epping Forest Survey: a preliminary account of the ecological work of the Chingford Branch at the Cuckoo Pits in 1942.' Lond. Nat. for 1942: 43–4.

Introduction to an ecological survey of the Cuckoo Pits area of Epping Forest, Essex, begun in 1942; with a map of the area.

London Natural History Society (1946). 'The survey of Bookham Common. Fourth Year.' Lond. Nat. No. 25, for 1945: 56–67. (Also as Lond. Nat. Repr. No. 35.)

This report contains an annotated list by A. M. Easton (pp. 56–63) of 202 weevils (Rhynchophora), mostly recorded from personal observation, with notes on methods of capture, which include sweeping the surface of water collected on the ground after heavy rain, and one by H. J. Burkill (pp. 63–7) of the galls associated with 76 plants based on data collected over 19 years, with special attention to those on oak.

Miles, M. (1948). 'Field observations on the bean seed fly (seed corn maggot), *Chortophila cilicrura*, Rond., and *C. trichodactyla*, Rond.' Bull. Ent. Res. 38: 559–74.

These larvae feed in Britain on beans, peas, cabbages, kale, cauliflowers, leeks, onions, cucumbers and lettuce. Diagrams illustrate the differences between the larvae of *Chortophila cilicrura* and *Hylemyia antiqua*. *Chortophila cilicrura* is on the wing from March to October and there is some evidence of slight activity during the winter. There are three to four generations a year. The peak periods of fly activity occur during mid-April to mid-May, late June to early July and in fine weather throughout August to October. Peak periods for larvae occur from mid-May to early June on beans, peas, cucumbers and cruciferous crops, during July on leeks and cruciferous plants and during September to November on spring cabbages. Natural enemies of *C. cilicrura* include a Staphylinid beetle, *Aleochara bipustulata* and a Hymenopterous parasite *Trybliographa diaphana*. The tiger fly, *Coenosia tigrina*, has been reared from predatory maggots found in beans with *Chortophila cilicrura* and larvae of Leptidae have also been found in beans with this fly.

Parmenter, L. (1942). 'The survey of Limpsfield Common. Fifth year. The Diptera of Limpsfield Common.' Lond. Nat. for 1941: 18–33.

Complete list, with many ecological details.

Parmenter, L. & Fitter, R. S. R. (1941). '[The Survey of Limpsfield Common. Fourth year.] A spring census of the birds of Limpsfield Common.' Lond. Nat. for 1940: 19–20.

Follows up winter censuses in 1938 and 1939.

Payne, L. G. (1945). ['The Survey of Bookham Common. Third year.] Coleoptera of Bookham Common: some extracts from my notebook, 1943.' Lond. Nat. No. 24, for 1944: 31–5.

Notes on the beetle fauna of the common, with many ecological details, but unfortunately in diary form.

Pinniger, E. B. (1946). 'The Neuroptera of the Home Counties.' Lond. Nat. No. 24, for 1945: 24–30.

Contains a table summarizing larval and adult habitats and larval prey of species occurring in Greater London.

Satchell, G. H. (1947). 'The ecology of the British species of *Psychoda* (Diptera: Psychodidae).' Ann. Appl. Biol. 34: 611–21.

Field dung, decaying vegetable matter and organic mud form the breeding places to one of which some species confine themselves, whilst others, e.g. *Psychoda severini*, breed in a variety of materials. *P. alternata* is more restricted in its choice and proved the best indicator of dispersal from sewage filters. With this fly, invasion of farms and woodland was apparent at distances of ¼ and 1 mile respectively from the filters, but not at a distance of 1½ miles in the direction of the prevailing wind. Among the parasites found are *Rhabdites curvicaudata*, an internal parasitic nematode allied to *Tylenchinema oscinella* and a protozoan parasite, probably *Glaucoma piriformis*.

Tucker, D. G. (Ed.) (1945). '[The Epping Forest Survey. Third year.] Report on the survey of the Cuckoo Pits area, 1942–44.' Lond. Nat. No. 24, for 1944: 39–65.

Deals with mammals, birds, reptiles, Amphibia, fish, Odonata, Lepidoptera, and plant galls by Hymenoptera, Diptera and Acarina.

(*d*) Small islands

Matthews, L. H. (1947). 'A note on *Crocidura russula* and other mammals in Alderney, Channel Islands.' J. Anim. Ecol. 16: 225.

Crocidura russula is the only shrew on Alderney, and does not have a differential distribution on the island, whereas Morrison-Scott reported that on Jersey, where *Sorex araneus fretalis* is also found, *Crocidura* was confined to the neighbourhood of the shore. The breeding season of this species is prolonged into late August on Alderney. Other mammals on the island were: *Apodemus sylvaticus*, *Mus musculus*, *Rattus rattus*, *R. norvegicus*, *Oryctolagus cuniculus*, and *Talpa europea*. Several small bats were seen.

Rogers, H. M. (1947). 'Ornithology of the Isle of Man, 1943, 1944, 1945.' Northw. Nat. 22: 45–61.

A systematic list of the birds observed, with dates, localities and notes on topics such as abundance and status, preceded by comments on the more interesting records.

2. GENERAL REPORTS AND TAXONOMIC STUDIES OF USE TO ECOLOGISTS

Soper, F. G. R. (1947). 'The study of natural history and archaeology in Bedfordshire (from 1798 to 1945).' J. Bedfordshire Nat. Hist. Soc. & Field Club, 1: 4–7.

The county's first flora was published in 1798, and its first natural history society founded in 1875; most of the natural history work in the county so far appears to have been floristic and faunistic rather than ecological.

Spooner, G. M. (1948). 'The British species of Psenine wasps (Hymenoptera: Sphecidae).' Trans. R. Ent. Soc. Lond. 99: 129–72.

Includes keys to genera, subgenera and species, as well as much information on biology, including nesting sites and parasites.

3. PARASITES

Day, C. D. (1947). 'British Tachinid flies (Tachinidae- Larvaevoridae and Calliphoridae).' Northw. Nat. for 22, Suppl.: 65–96.

This part concludes the key to primary group 20 and contains the keys to primary groups 21–36, as well as 19 tables of species of the larger genera, the last of which is to be continued.

Harvey, John H. (1944). 'Observations on the parasites of the cabbage butterflies.' Lond. Nat. for 1943: 12–19.

The larvae of the butterflies *Pieris brassicae* and *P. rapae* are parasitized by *Apanteles glomeratus*, and their pupae by *Pteromalus puparum*. *Apanteles* is in turn parasitized by *Hemiteles fulvipes*, *Dibrachys cavus* and *Tetrastichus rapo*. Detailed personal observations on the life histories of these are given.

Hickey, M. D. & Harris, J. R. (1947). 'Progress of the *Diphyllobothrium* epizootic at Poulaphouca Reservoir, Co. Wicklow, Ireland.' J. Helminth. 22: 13–28.

The annual mortality occurring in trout (*Salmo trutta*) during the summer was caused by peritonitis attributed to the plerocercoids of *Diphyllobothrium dendriticum* becoming active as a result of increase in temperature. *D. dendriticum* was found in avian hosts which fed mainly on dead or dying trout, *D. ditremum* only in those which caught live trout. The trout are probably infected by feeding on sticklebacks (*Gasterosteus*) primarily infected from *Cyclops strenuus abyssorum* and *Diaptomus gracilis*. Feeding experiments on birds and mammals are recorded.

Jolley, A. E. & Storer, R. [1945]. 'Report on the sand-martin enquiry, 1944.' Leicestershire & Rutland County Rep. on wild Birds for 1944: 10–21.

Deals mainly with the breeding biology of *Riparia riparia* but a section on parasites covers *Microglossa pulla* (a beetle found in the nests), *Ceratopsyllus styx* (a flea), and *Ixodes erinaceus* (a tick).

McLauchlan, J. D. & Henderson, W. M. (1947). 'The occurrence of foot-and-mouth disease in the hedgehog under natural conditions.' J. Hyg., Camb. 45: 474–79.

Diseased hedgehogs were found in connexion with outbreaks of foot-and-mouth disease among farm stock in Norfolk in the summer of 1946. It may be fatal to the hedgehog and it seemed probable that affected hedgehogs were responsible in some instances for spreading the disease to cattle.

Neal, R. A. (1948). '*Entamoeba histolytica* in wild rats caught in London.' J. Hyg., Camb. 46: 90–3.

Rats had become infected by a local human infection of *Entamoeba histolytica*. Infection produced experimentally in rats responded to treatment with emetine hydrochloride.

Yarrow, I. H. H. (1941). '*Andrena* and *Nomada* (Hymenoptera, Apidae) on Hampstead Heath.' Lond. Nat. for 1940: 9–13.

Of the British species 58 % of the host (*Andrena*) and 66 % of the parasite (*Nomada*) have been recorded for the area, on which large exposed areas of Bagshot sand provide an ideal nesting ground for the host species. Other ecological details are given, e.g. the preference for hard footpaths shown by *Andrena armata*.

4. FOOD AND HABITS

Anscombe, F. J. & Singh, B. N. (1948). 'Limitation of bacteria by micro-predators in soil.' Nature, Lond. 161: 140–1.

Eight micropredators (two unidentified species of amoebae, *Leptomyxa reticulata*, myxamoebae of two species of *Dictyostelium* and three species of Myxococcaceae) showed a tendency to feed on the same selection of host bacteria (87 strains considered). Three pairs of the predators showed highly similar selections. Two pairs showed a preference for Gram-negative bacterial strains and would thus tend to be complementary to many soil organisms which prefer Gram-positive bacteria.

Barnes, H. F. (1948). 'Gall midges of economic importance. Vol. III: Gall midges of fruit.' 184 pp., 9 photo-plates. Crosby Lockwood & Son Ltd., 20 Tudor Street, London, E.C. 4. Price 15*s*.

This monograph covers all the known gall midges (Cecidomyiidae) associated with cultivated fruits, or commercially important wild fruits (both bush and tree), in the world. It describes succinctly the appearances of damage and what is known about biology, life histories and control, but does not cover the taxonomy itself, except to give full references to the literature relevant to each species. Attention is drawn to the difficulty of deciding specific limits in the case of forms that attack different fruit trees though looking almost or exactly similar morphologically. The author points out the importance of knowing exact seasonal dates of the life history and habits, for planning effective control measures.

Burkill, H. J. (1943). '*Cucullia verbasci* and its food plants.' Lond. Nat. for 1942: 26–7.

Experiments on the food preferences of the mullein moth.

Burkill, H. J. (1944). 'Plant gall records for 1943.' Lond. Nat. for 1943: 8–9.

Includes records for Cynipidae, Cecidomyiidae, Muscidae, Aphididae, Acari, Eriophyidae and Nematoda. See also reports by the same author in (1941), Lond. Nat. for 1940: 17–18; and (1942), Lond. Nat. for 1941: 13–14.

Burkill, H. J. (1945). 'Plant gall records for 1944.' Lond. Nat. No. 24, for 1944: 14.

Includes records for Cecidomyiidae, Muscidae, Aphididae and Eriophyidae.

Burkill, H. J. (1946). 'Plant gall records for 1945.' Lond. Nat. No. 25, for 1945: 47–8.

Includes records for Cynipidae, Chalcidides, Trypetidae, Cecidomyiidae, Eriophyidae and Nematoda.

Clark, J. G. D. (1948). 'The development of fishing in prehistoric Europe.' Antiquaries Journal, 28: 45–85.

A comprehensive review of the types of fishing gear used by prehistoric man in Europe, and of the evidence for the types of fish eaten by him—eel, flounder, pike, roach, cod, conger, coal-fish, dogfishes, grey mullet, haddock,

ling, rays, sea-bream and species of wrasse, as early as Mesolithic times; burbot, carp, perch, pike, roach, salmon by the lake-dwellers, also eels and probably sturgeon, in Neolithic times. The herring, so important economically to-day, is conspicuously absent from the prehistoric remains. Three appendices give a list of prehistoric sites in Northern Europe and Britain and of the species of fish and kinds of fishing gear found at each of them.

Department of Health for Scotland (1946). 'Control of midges: an Interim Report of a Sub-committee of the Scientific Advisory Committee.' 11 pp. H.M. Stationery Office, Edinburgh. Price 2*d*.

Midges of the genus *Culicoides* often cause very serious irritation to man, and in Scotland *C. impuncatus* is the commonest species and accounts for the majority of bites on man. It breeds in soil. There are 14 other species in Scotland. The common species was used for tests of ointments containing DMP (dimethylphthalate), which was partly successful as a repellent. Veils impregnated with DMP were very successful. An appendix to the Report gives convenient summaries of the distribution and habits of all the species in Scotland, so far as they are known.

Department of Health for Scotland (1948). 'The Second Report on control of midges by a Sub-committee of the Scientific Advisory Committee.' 11 pp. H.M. Stationery Office, Edinburgh. Price 4*d*.

The usefulness of DMP ointments against midges was confirmed, but the ointment must contain not less than 40% by volume of the DMP and the latter must be of stable quality. Impregnated veils also proved successful again. The ointment was not repellent to the harvest mite (*Trombicula autumnalis*) or to ordinary non-biting flies. The Report assembles information about the ecology of *Culicoides impunctatus* and other less common species, discusses methods of trapping adults emerging from the soil, notes that domestic animals are also the prey of certain species, and affirms that the presence of midges in some Highlands districts can actually hold up farming sometimes, and is certainly a bar to holiday visiting and camping. A sample of 6000 midges from the Trossachs consisted of 96% *C. impunctatus*, the rest being *C. obsoletus* and *pallidicornis*. Other definite man-biters in Scotland are *C. heliophilus*, *pulicaris*, *grisescens* and *delta*. Human reactions to bites vary considerably in different individuals.

Fenton, G. R. (1947). 'The soil fauna: with special reference to the ecosystem of forest soil.' J. Anim. Ecol. 16: 76–93.

The methods used in sampling the whole soil fauna range (micro-, meso-, and macrofauna) are outlined, and methods applicable to the mesofauna are discussed in detail. Direct sorting, sieving, flotation, automatic, centrifuging and wetting methods are described. Soil animals are grouped according to their food habits and effects on the soil, under the following heads: Ectophagous animals, Endophagous animals, 'Chemical agents', Predators, 'Secondary Product Eaters', and Shelterers. The Lumbricidae are the only group about whose ecology anything has been done from this aspect. The role of the mesofauna in effecting the distribution of humus (an important reservoir of plant food) in the soil is described. The calcium content of leaves, related to their palatability, is suggested as a factor determining the distribution of the mesofauna. Mull and podsol formation is described, with reference to the work of Müller, Bornebusch and Jacot. The part played by animals in the nitrogen cycle and their action in speeding up and possibly determining the course of decay is outlined, and the assimilation of nitrogen by the plant is touched upon. An extensive bibliography of publications dealing with the soil fauna and related ecosystems is appended.

Jones, D. P. & Jones, F. G. W. (1947). 'Wireworms and the sugar-beet crop: field trials and observations.' Ann. Appl. Biol. 34: 562–74.

Observations on wireworms in the sugar-beet crop during 1937–40 indicated the importance of alternative food, such as buried turf, weeds, excess seedlings and interdrilled wheat in determining the degree of injury to the crop.

Jones, D. P., Petherbridge, F. R. & Jenkins, A. C. (1947). 'Beet carrion beetle in England and Wales.' J. Minist. Agric. 54: 375–7.

The adult beetle and the larvae of *Aclypea* (*Blitophaga*) *opaca* feed on sugar-beet, mangolds, oats, barley, wheat, swedes, turnips, potatoes, cabbage and many other plants. They exhibit a slight preference for plants of the Chenopodiaceae. Includes notes on life cycle.

Lees, J. L. (1948). 'Winter feeding hours of robins, blackbirds and blue tits.' Brit. Birds, 41: 71–6.

Analysis of the times at which birds were trapped for ringing during the winter show that the robin (*Erithacus rubecula*) has two feeding peaks, one just after sunrise and another just before sunset; the blackbird (*Turdus merula*) on the other hand has two peaks very close together, just before and after midday; the blue tit (*Parus caeruleus*) is intermediate between the other two species.

Lilly, A. H. R. (1947). 'Investigations on the gout fly (*Chlorops pumilionis* Bjerk.) in Devon and Cornwall.' Ann. Appl. Biol. 34: 551–61.

In Devon and Cornwall this fly shows a definite preference for oviposition on wheat rather than on barley or couch grass. Flies emerge from October-laid eggs during May while the second generation flies appear in late July and early August. These latter flies do not oviposit until two months later. The result is that wheat not above ground before 20 October (drilled after 12 October) escapes attack. The flies prefer young growth, i.e. young tillers, on which to oviposit. It is suggested that there is a biological strain of gout fly with a definite preference for wheat.

Newstead, R. (1947). 'Food of the pygmy or lesser shrew (*Sorex minutus* Linn.).' Northw. Nat. 22: 103–4.

The stomach contents of three pygmy shrews trapped in North Wales in September 1943 comprised the remains of numerous Arctiid moth larvae, a moth, three gall-making mites of the genus *Eriophyes* and a Staphylinid beetle, and in three trapped in December were found the remains of a beetle (*Aphodius*?), very many *Siphonophora* [= *Macrosiphum*, aphid], and an Arctiid larva; hairs from the bodies of the shrews were also present. The shrews were caught in nipper traps baited with cheese, and used the same runways and entrance holes as field mice.

Synge, A. D. (1947). 'Pollen collection by honeybees (*Apis mellifera*).' J. Anim. Ecol. 16: 122–38.

Pollen brought in by colonies of bees at Rothamsted during 1945 and 1946 was collected daily in pollen traps and analysed into constituent pollen species. Seasonal occurrence of different pollens was also analysed. About 100 plants were found to be used for pollen collection; legumes (54%) rosaceous trees and shrubs (15%) and forest trees (11%) yielded 80% of the total pollen for 1946. The floral mechanism making pollen available to the bee was investigated for various plant species, and a connexion between the time of day that pollen is available and the time of its collection by bees is demonstrated. A correlation was also found between the number of loads of red clover pollen gathered and the daily maximum temperature: more flowers being open at higher temperatures. Large differences between two neighbouring colonies of bees in the same apiary were found when amounts of pollen gathered from different plant species were compared. Three colonies, offered a choice of pollen within the hive, showed a preference for white clover over red clover, *Brassica*, *Onobrychis*, and *Papaver*.

5. POPULATION STUDIES

Brady, F. [1944]. 'The breeding bird population of the Brand.' Leicestershire & Rutland County Rep. of Wild Birds for 1943: 9–12.

The Brand is a private estate on the fringe of Charnwood Forest, and its bird population was surveyed in 1940 and again in 1943; the number of breeding pairs fell from 212 to 192, but the species represented rose from 35 to 39 between these years.

Brian, M. V. (1947). 'On the ecology of beetles of the genus *Agriotes* with special reference to *A. obscurus*.' J. Anim. Ecol. 16: 210–24.

An inquiry into the habits, distribution, and reproduction of *Agriotes* spp. in their normal habitat. An attempt is made to assess the chance of survival and reproduction should that environment be abruptly changed by cultivation. Studies of movement by walking in grassland using a new electronic detector method proved practicable. A pot experiment was carried out to test the effects of eight crops on fecundity and longevity.

Brian, M. V. & Brian, A. D. (1948). 'Regulation of oviposition in social Hymenoptera.' Nature, Lond. 161: 854.

In nests of *Bombus agrorum* eggs were laid only on pupal cells—usually three days after their formation and about three eggs per pupa. In ant colonies (*Myrmica* spp.) oviposition tended to increase soon after metamorphosis started, but there was no quantitative relation between numbers of pupae and eggs as in the bumble-bee.

Broadbent, L. (1947). 'An analysis of captures of Aphididae (Hemiptera) in a light trap.' Trans. R. Ent. Soc. Lond. 98: 475–90.

Four years' captures are analysed on arithmetic and logarithmic bases, month by month and throughout the night. Aphids were flying by night from May to November. Activity was positively correlated with the maximum temperature of the previous day and with the evening reading of the dew-point. It was negatively correlated with the wind force of the previous afternoon. Wind direction had a significant effect. Population changes from year to year were probably dependent to a large extent on the summer rainfall, the population being lower in wet years.

Brown, P. E. & Allen, E. Lynne- (1948). 'The breeding of avocets in England in 1947.' Brit. Birds, 41: 14–17.

Records the establishment of two colonies of breeding *Recurvirostra avosetta* in East Anglia after about a century during which only very occasional single pairs were known to breed.

Bruce, H. M. (1947). 'The feeding and breeding of laboratory animals. VI. The breeding of mice.' J. Hyg., Camb. 45: 420–30.

1149 albino mice were weaned by 24 females in one year under a system of monogamous pairing where the male was kept continuously with the female, in 78% of cases the females became pregnant again at post-partum oestrus, as compared with 559 under a system of polygynous mating where several females kept with one male, were removed for the birth of litters and returned when they had weaned their young. Maturity was reached at about 2 months, gestation varied from 17 to 22 days, the normal period being 19 days. Litter size, mortality and sex-ratio were alike under both systems. One monogamous female produced 16 litters in succession, 15 from post-partum oestrus matings, but the litters were small, only 51 young were weaned as compared with the maximum of 121. The female reproductive rate declines with age, particularly from 8 to 9 months of age. The interaction of concurrent gestation and lactation upon the length of gestation is discussed.

Duffey, E. A. G. [1947]. 'The change in bird-life during the growth of a Charnwood conifer plantation.' Leicestershire & Rutland County Rep. of Wild Birds for 1946: 9–13.

A study carried out over 11 years, divided into two stages. From the second to the seventh year ground- and scrub-nesting birds were dominant. From the eighth year onwards their place was gradually taken by tree-nesting species requiring cover and secondary growth.

Fitter, R. S. R. (1943). 'The starling roosts of the London area.' Lond. Nat. for 1942: 3–23.

A full survey of existing knowledge of the origin and extent of the roosting of *Sturnus vulgaris* in inner London, where a notable feature is that many of the roosts are on buildings, as well as in the surrounding countryside. Roosting in inner London was first recorded in 1894, prior to which London starlings flew out to the country to roost; the pattern of roosting in this species around London has since changed to such an extent that inner London now draws all the winter population of starlings from a radius of 5–12 miles around.

F[itter], R. S. R. (1943). 'Black redstarts in London and Middlesex in the summer of 1942.' Lond. Bird Rep. for 1942: 17–20.

The black redstart (*Phoenicurus ochrurus*) is in process of colonizing southern England. In London and Middlesex in 1942 at least three pairs bred, four other pairs were present but not proved to have nested, and between 16 and 23 other singing males were present.

F[itter], R. S. R. (1944). 'Black redstarts in the London Area in the summer of 1943.' Lond. Bird Rep. for 1943: 17–19.

During the 1943 breeding season three pairs of *Phoenicurus ochrurus* bred in the City of London, and some 16 other singing males were present in other parts of the London area.

Fitter, R. S. R. (1945). 'Black redstarts in the London Area in the summer of 1944.' Lond. Bird Rep. No. 9, for 1944: 19–21.

Five pairs of *Phoenicurus ochrurus* bred in the London area during the year, and at least six other singing males were present.

Fitter, R. S. R. (1946). 'Black redstarts in the London Area in the summer of 1945.' Lond. Bird Rep. No. 10, for 1945: 25–6.

Two or three pairs of *Phoenicurus ochrurus* nested in the City of London during the year, and ten singing males were present in inner London.

F[itter], R. S. R., P[arrinder], E. R. & A[shby], C. B. (1946). 'A rookery census of the London Area.' Lond. Bird Rep. No. 10, for 1945: 22–3.

A census carried out in conjunction with the British Trust for Ornithology showed a provisional figure of 9971 nests of *Corvus frugilegus* in 355 rookeries. The nearest rookery to St Paul's Cathedral was at Lee Green, 6½ miles away, and only three small rookeries remained within 10 miles of this central point.

F[itter], R. S. R., P[arrinder], E. R. & A[shby], C. B. (1946). 'The Heronries of the London Area.' Lond. Bird Rep. No. 10, for 1945: 23–4.

The known number of nests of *Ardea cinerea* in the London area fell from 138 in 1939 to 104–6 after the severe winters of 1940–2, but rose again to 165 in 1945.

Haarløv, N. (1947). 'A new modification of the Tullgren apparatus.' J. Anim. Ecol. 16: 115–21.

A description and illustration of the apparatus is given. It was used for both qualitative and quantitative collecting of Collembola and Acarina in samples of a surface area of 0·001 sq.m. and a depth of 6–7 cm. The operation of the apparatus and sources of error are described, and an account given of the results obtained with it.

Höhn, E. O. (1946). 'Some recent observations on starling roosts in the London Area.' Lond. Bird Rep. No. 10, for 1945: 26–8.

Discusses previously advanced theories that *Sturnus vulgaris* forsakes tree roosts for buildings at the time of leaf-fall in the autumn, and that the birds that roost in London are of Continental origin.

Houghton, A. T. R. (1948). 'Industrial pollution in the Ribble: how it has affected the salmon runs.' Salm. Trout Mag. No. 123: 141–6.

Up to 1944 the actual catch of salmon in the River Ribble (Lancashire) accorded with predictions based on a 4-year cycle. There was a considerable divergence in 1945 and 1946 and it is suggested that the cause was industrial pollution.

Keighley, J. & Lockley, R. M. (1948). 'The incubation and fledging-periods of the razorbill.' Brit. Birds, 41: 113–14.

Alca torda has a mean incubation period of 34 days and a fledging period of about 16 days.

Lack, D. (1948). 'Notes on the ecology of the robin.' Ibis, 90: 252–79.

Evidence relates the winter distribution of the robin *Erithacus rubecula*, (mainly wood edge, gardens and hedgerows) to the greater mortality from hard winters in, for example, the middle of woods. Analysis of ringing data shows that the expectation of life in European migrants is slightly less (0·8 years) than in the British bird (1 year), and this corresponds with a difference in mean clutch size between the two areas. Although primarily insectivorous, the robin takes a wide range of foods and any selectivity shown is probably more by the method of feeding (pouncing down upon ground fauna from a perch) than by any particular preferences.

Lack, D. (1948). 'Further notes on clutch and brood size in the robin.' Brit. Birds, 41: 98–104, 130–7.

Supplement to data published in the same journal in 1946. Analysis of clutch-size records according to season shows that the number of eggs rises to a peak in April and May and falls again in June. Annual and regional differences are also discussed. Nesting success is greater in May than either before or after, but there is no proof that larger clutches have proportionately smaller fledging success.

Le Cren, E. D. (1947). 'The determination of the age and growth of the perch (*Perca fluviatilis*) from the opercular bone.' J. Anim. Ecol. 16: 188–203.

From the results of work at Windermere it is concluded that the use of the opercular bone provides a good general method for ascertaining the age and growth of the perch. Readings of age from the opercula of fish up to 4 years old at least, agree with estimates of age made from length-frequency distributions, and are also confirmed by the occurrence of dominant year classes in successive annual samples. The opercular shows allometric growth in relation to the length of the fish. The correction of directly proportionate back-calculations of growth is described. There is little direct evidence to check the accuracy of these back-calculations, but evidence available shows them to be reasonably accurate in general.

Parrinder, E. R. (1948). 'The little ringed plover in the London area in 1947.' Brit. Birds, 41: 41–5.

This recently established breeding species, *Charadrius dubius* nested in the neighbourhood of London in increased numbers in 1947, 11–14 pairs being recorded.

Varley, G. C. (1947). 'The natural control of population balance in the knapweed gall-fly (*Urophora jaceana*).' J. Anim. Ecol. 16: 139–87.

A detailed census of a series of 92 sq.m. plots from an area near Cambridge was carried out to determine what factors control the population density of the knapweed gall-fly in nature, and how they operate. The use of Nicholson and Bailey's theory of 'balance of animal populations' to analyse the results obtained in the census gave a picture of the mutual effect of parasitic and other factors of destruction on the population density of an insect in nature. Population density, fecundity, and mortality affecting the different stages were estimated;

three of the factors which keep the population in balance were found to be affected in their severity by the population density in which they were acting. These were the early larval mortality, the chalcid parasite *Eurytoma curta* and the chalcid parasite *Habrocytus trypetae*. Non-specific mortality occurred, decreasing the efficiency of *Eurytoma curta* as a controlling agent. All mortality factors do not necessarily tend to reduce the mean populations on which they act. The census data are interpreted as a glimpse of irregular oscillations occurring about the steady state.

Wright, D. W. & Geering, Q. A. (1948). 'The biology and control of the pea moth, *Laspeyresia nigricana*, Steph.' Bull. Ent. Res. 39: 57–84.

Includes emergence dates, field abundance, behaviour of moths and larval populations in the field, behaviour of larvae in the soil, effect of soil temperatures on the development of the overwintering larvae. Other host plants include *Lathyrus pratensis*, *L. odoratus*, *Vicia cracca* and *V. sativa* in order of high to low percentage pod attack. Three Hymenopterous parasites were reared from the larvae: *Ascogaster quadridentatus* (Braconid), *Glypta haesitator* and *Hemiteles ridibundus* (Ichneumonids).

6. MIGRATION, DISPERSAL AND INTRODUCTIONS

Bartlett, T. L. (1944). 'Recoveries of black-headed gulls in inner London.' Lond. Bird Rep. 1943: 19. (See also (1946) Lond. Bird Rep. for 1945: 20.

Larus ridibundus tends to be recovered at the same place in Inner London at which it was ringed, indicating constancy of feeding station.

Cain, A. J. & Cushing, D. H. (1948). 'Second occurrence and persistence of the amphipod *Orchestia bottae* M. Edwards in Britain.' Nature, Lond. 161: 483.

This Mediterranean species was first found on the banks of the Thames at Richmond in 1942. In 1946–7 it was found at Oxford, 92 miles upstream from the first lock at Teddington.

Gibb, J. (1948). 'Report on the immigration of waxwings, winter, 1946–7.' Brit. Birds, 41: 2–9, 34–40.

Observations from all parts of the British Isles showed that the invasion of *Bombycilla garrulus* commenced in Scotland in October and the birds moved south into England during the winter. There is a summary with much information on food.

Gimingham, C. T. & Thomas, I. (1948). 'Colorado beetle in England, 1947.' J. Minist. Agric. 55: 55–63.

Twelve colonies of *Leptinotarsa* on potatoes and 13 single beetles in different places during 1946. More colonies (57) were discovered in England during 1947 than in any previous year. A considerable number of beetles were found with imports from the Continent during the earlier part of the year. Maps are given of the isolated finds and the breeding colonies. The latter occurred in Leicester (1), Northampton (1), Cambridge (1), Bedford (6), Buckingham (1), Hertford (5), Essex, (2) Middlesex (1), Surrey (5), Kent (33) and Sussex (1).

Reid, D. M. (1948). 'Occurrence of the amphipod *Orchestia bottae* and other organisms in Britain.' Nature, Lond. 161: 609.

It is suggested that this amphipod is not a late immigrant from the Continent but that knowledge of its range is increasing. *Eucrangonyx gracilis* and *Gammarus lacustris* also appear to have a more established distribution than might appear from the late discovery of their range.

Small, T. (1948). 'Colorado beetle in Jersey, 1947.' J. Minist. Agric. 54: 569–74.

In 1946 only 36 adult *Leptinotarsa* were found, in 1947 only 4 adults were found on the sites of the old outbreaks. But at the end of May 1947 a heavy invasion occurred, presumably from France, with the result that 742 live beetles were reported. Includes notes on incidence of larvae.

7. REPORTS OF ORGANIZATIONS

Blundell's School Science Society Magazine (1947). No. 2, 48 pp.

Short papers include: notes on the butterflies of the Tiverton area, the flora of a marsh-meadow, an ecological study of a field drainage system with special reference to colonization, factors affecting the local distribution of the mayfly (*Ecdyonurus* sp.), and a survey of the marine algae of Guernsey. The latter includes a list of species recorded and notes on ecological factors and distribution.

British Trust for Ornithology (1948). Fourteenth Report. 24 pp.

Contains brief summaries of current co-operative inquiries and a statement on the organization, staff and research projects of the Edward Grey Institute. The latter include: hatching and fledging inquiry, sample heronry census, black redstart inquiry, sample great crested grebe census, the opening of milk-bottles by tits, swift migration, redwing migration, and a supplementary rook census.

Éire, Department of Agriculture, Fisheries Branch [1947]. 'Salmon, sea trout and eels captured in Éire during each of the six years 1946, 1945, 1943, 1941, 1939 and 1937.' Dublin, 17 pp. Price 6*d*.

Consists of ten tables giving the catch in each fishery district.

Éire, Department of Agriculture, Fisheries Branch [1947]. Report of the Minister for Agriculture on the sea and inland fisheries for the year 1946. Dublin, 30 pp. Price 9*d*.

Sea fisheries for 1946 recorded catches that equalled the large returns of 1945. Inland fisheries for salmon showed an increase over the low yield of 1945, although small spring fish were abnormally scarce and the decline in the runs of large spring fish, noticeable since 1937, continued during 1946.

Goddard, T. Russell [1947–8]. Ornithological Report on the Farne Islands for 1947.

Common eider (*Somateria mollissima*) nested in numbers again, in spite of a suspected slaughter of Northumberland birds for the market in 1946. Some interesting notes on the beneficial effects of excluding the general public from Inner Farne, where both birds and vegetation improved their position. Details about various species of birds on the Islands.

Lancashire and Cheshire Fauna Committee [1948]. 'Twenty-seventh Report and Report of the Recorders for 1943–46.' Arbroath. 70 pp.

Besides various notes on range, occurrence and habitats of vertebrates, and different insect groups, this Report devotes a good deal of space to marine, brackish and freshwater Crustacea, and to Rotifera.

Lundy Field Society [1948]. First Annual Report, 1947. 19 pp. Price 2*s*.

The first year of operation of this Society has been largely spent in preliminary surveys of the habitats of the island. A list of bird species and special records of autumn migrants are given.

Yorkshire Fishery District (1948). Eighty-first Annual Report on the salmon, trout and freshwater fisheries in Yorkshire (1947) (by R. W. Ward). 37 pp.

The total catch of salmon and sea-trout was 1088 fish. No figures are available for other species but there appear to be fair stocks in the rivers of the county. A description of the new fish hatchery is given.

Wye Board of Conservators (1946). Annual Report, Season 1945. 11 pp. (1947), ibid. 1946, 11 pp. (1948), ibid. 1947. 13 pp.

Contain details of the rod and net catches of salmon, the spawning conditions and effects of weather; also indications of the population structure and relation to previous fluctuations. Minor notes on other fish. By the River Boards Bill the Wye Board of Conservators will shortly cease to exist as such, after 80 years' existence; but it appears that the new centralized control of rivers will still allow room for committees to be appointed to handle specialized matters such as fishing, wild life and pollution. The Wye Board (A.R., Season 1945) won probably the first pollution case in which the prosecution was for injuring 'the food of fish' (by chemical effluents).